

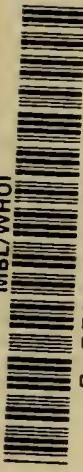
**SIMPLE HOLOCARPIC  
BIFLAGELLATE PHYCOMYCETES**

**JOHN S. KARLING**

*Columbia University*



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# THE SIMPLE HOLOCARPIC BIFLAGELLATE PHYCOMYCETES

Including a  
Complete Host Index and Bibliography

BY

JOHN S. KARLING

*Columbia University*

FIRST EDITION



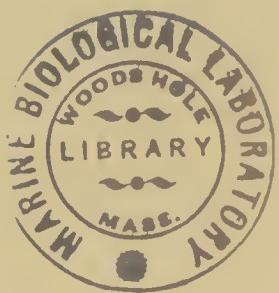
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Dedicated to the Memories of  
**SCHENK, CORNU, AND ZOPF**

For their Contributions to the  
Knowledge of the Lower Fungi





## PREFACE

THIS SMALL volume on the simple, holocarpic, biflagellate Phycomyctes is the second in a series of lectures presented to graduate and research students of mycology at Columbia University on the origin, development, phylogeny, and evolution of the lower organisms. These simple Phycomyctes, with the exception of the Lagenidiaceae, were formerly included in the Clytridiales by most mycologists, but with the recognition in recent decades that the number, position, and relative lengths of the flagella are of fundamental phylogenetic significance, the viewpoint has gradually developed that these species cannot be incorporated in the same order with the posteriorly uniflagellate chytrids. On the basis of present-day evidence, the author concurs with this belief and is accordingly presenting these biflagellate species apart from the chytrids. Many of these simple fungi exhibit distinct oomycetous characters and tendencies and should perhaps be included directly in existing or new families of the Phycomyctes, while the life cycles of other species suggest a relationship or at least a parallelism in development with the Plasmodiophorales and Protoomyxa. It is thus impossible at present to include all of them in one family or order and very difficult to assign them to a definite position in a natural system of classification. For this reason they are treated separately and are referred to here as a heterogeneous collection of simple, holocarpic, biflagellate Phycomyctes. This long title is obviously inadequate and can also be extended to include other Phycomyctes not discussed here, the thalli of which may sometimes be holocarpic. A more adequate and briefer title is not available, although the descriptive name Holobiflagellomycetes is suggested. The use of the term "simple" is not to be interpreted as meaning that these fungi are primitive and have given rise directly to the higher Oomycetes and Zygomycetes. Nor does the author wish to convey the impression that by discussing these diverse fungi under one title that he considers them as constituting a natural phylogenetic series. Whether or not they comprise several distinct families is obviously open to question. The family Woroninaeae, for example, includes several dissimilar genera and is very doubtful. Should the type species *Woronina polycystis* prove to be a member of the Plasmodiophorales, as seems quite likely at present, the former family name would no longer be tenable. The author has nonetheless grouped the genera in five families, realizing fully that the grounds for doing so are woefully inadequate. Mycologists will doubtless disagree with

this arrangement, but in our state of meager knowledge concerning many of the genera and species, classification into families is not so important at present, in the author's opinion, as making available to research students all known facts and data.

These fungi have been the subject of study for almost a century, but no serious attempt has been made to summarize the widely scattered data in zoological and botanical journals. Fischer ('92), Schroeter ('97), and Minden ('11) discussed rather fully the species known at the turn of the century, but since that time most textbooks of mycology have given scant attention to them. During the past two decades several new genera and species have been discovered, and additional intensive studies on long known species have modified our concepts of host range, sexuality, relationships, etc., within the group. In light of these discoveries and the fact that these simple holocarpic fungi are so significant from the standpoints of phylogeny and evolution of the higher Phycomyctes, the author believes that a separate and complete treatment of them is very essential and worthwhile, particularly in stimulating research. A full discussion of the doubtful and excluded species is also presented with the purpose of making these data available to research workers. Although the author agrees with the view that *Achlyogeton*, so far as it is now known, should be excluded because of its reported posteriorly uniflagellate zoospores, he nevertheless believes it may possibly prove to be a valid member of the group.

In the text which follows very few technical terms are used. A glossary is accordingly unnecessary and has been omitted. Separate bibliographies are provided at the end of each chapter to expedite reference to the literature on particular subjects, genera, and species. A host index of plant and animal genera and species, together with an inclusive bibliography, is presented in the final chapter. Due to war conditions, many of the recent European and Asiatic journals have not been available, so that this index and bibliography may not be complete. The illustrations of numerous authors in America and other parts of the world have been freely used by the author. Grateful thanks for this courtesy is hereby expressed to them. These contributors are too numerous for individual mention, but full credit for their drawings is given in the descriptions of the plates.

COLUMBIA UNIVERSITY  
NEW YORK CITY  
OCTOBER, 1912



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## Introduction



THE FUNGI presented herewith as the simple, holocarpic, biflagellate Phycomyctes comprise a heterogeneous collection of approximately eighty species which are characterized by relatively small or reduced, holocarpic thalli and biflagellate zoospores. Although these characters are common to all members of the group, present day evidence does not fully warrant the inclusion of these species in one coherent family or order. The simple species were formerly included by most mycologists in the family Woroninaceae and placed among the Chytridiales, while the elongate, more mycelioid members were incorporated in the Lagenidiaceae and regarded as closely related to the Saprolegniaceae and Pythiaceae. Inasmuch as the Chytridiales are characterized by posteriorly uniflagellate zoospores, the members of the Woroninaceae can no longer be included in this order as it is now recognized. For this reason these biflagellate species as well as the Lagenidiaceae are described apart from the chytrids. As will become evident below, they do not constitute a well-defined order or family and it is accordingly impossible to give the group as a whole a distinctive name. They are thus presented as simple, holocarpic, biflagellate Phycomyctes. The majority of them are Oomycete-like and appear to be either simple and primitive or reduced and degenerate Oomycetes, but since some species are reported to be isogamous, like the Zygomycetes, they must for the time being be listed under the more general term Phycomyctes. Further study of known species and the discovery of new ones will doubtless invalidate many of the present day concepts concerning their phylogeny and relationships, and it is not improbable that they may eventually be included in existing families and orders of the Oomycetes and Zygomycetes.

Whether or not the known genera and species comprise several distinct and clearly defined families is not at all certain at the present time. The critical developmental stages of many species are unknown, and the limits of the genera are not sharply defined. Nevertheless as an aid in classification and an expedient of reference, they have been grouped into five families on the basis of thallus structure and method of sexual reproduction. The structure of the vegetative thallus alone is obviously of questionable diagnostic value, but in species where resting spores and sexual reproduction are unknown, it is the only basis of distinction for the present. The order in which the families are presented does not always indicate degree of complexity, phylogenetic relationship, and evolution. The provisional family Woroninaceae is presented first because of its plasmodium-like thallus and

other structural similarities it has in common with the Plasmodiophorales, but the second family, Ectrogellaceae, shows distinct saprolegniaceous characteristics by its diplanetic zoospores. How closely this family is related to the Saprolegniales cannot be ascertained at present, because so little is known about its resting spores or the occurrence of sexuality. The Olpidiopsidaceae should perhaps be placed next to the Lagenidiaceae because of its predominantly heterogamous type of sexual reproduction. The Sirolpidiaceae, however, is placed in this relative position because its thallus has a tendency to become elongate, filamentous, mycelioid and fragmented like that of some species of *Lagenidium* and *Myzocytium*. On the other hand, its thallus may sometimes be reduced and distinctly olpidioid. The occurrence of such thalli and the fact that nothing is known about the type of sexual reproduction makes the position of this family next to the Lagenidiaceae very problematical. The Lagenidiaceae appears to be the most complex as far as thallus structure and method of sexual reproduction are concerned and is accordingly presented as the highest family in the evolutionary series. In most species the thallus is elongate and often distinctly mycelioid, but it may also be reduced, unicellular, and olpidioid. However, the resting spores or oospores are usually developed in partially or fairly well differentiated oogonia as in the higher Oomycetes.

The simpler, olpidioid species were discovered shortly before the middle of the last century. Although they had probably been observed earlier, Nägeli ('44) was among the first to describe and illustrate them as globular bodies in the mycelium of water molds, but he mistook them for a part of the normal life cycle of the host. Cienkowski ('55) likewise misinterpreted the parasites which he found in *Achlya prolifera* as a third type of sporangia developed by this host, but in the same year the parasitic nature of these intramatrical bodies was clearly recognized by Alexander Braun. The species which he described in *Saprolegnia ferox* is now believed to relate to *Olpidiopsis Saprolegniae*. He named this parasite *Chytridium Saprolegniae* and placed it in his sub-genus *Olpidium* of the Chytridiaceae. Thus, at an early stage these *Olpidiopsis* parasites became associated with the chytrids in mycological literature, and this fact together with their striking similarity of thallus structure and type of development to that of the olpidioid chytrids are probably the chief reasons why most mycologists up to the present time have included them in the Chytridiales. Despite Braun's excellent study Pringsheim ('60) was still doubtful about the nature of these parasites and believed that they might possibly be the antheri-

dia of *Saprolegnia*. However, an intensive study by Cornu in 1872 settled forever the question of whether they are parasites or relate to the life cycle of the host. He proved conclusively their parasitic nature and established the genera *Olpidiopsis* and *Woronina* for the biflagellate species which occur in *Achlya*, *Aphanomyces*, and *Saprolegnia*. Like Braun he included these parasites in the Chytridiales. Cornu observed that the resting spores were usually accompanied by one or more attached, thin-walled, empty vesicles which he assumed to be male cells or antheridia. In 1878 Reinsch observed the passage of the protoplasm of the small cell into the larger one, and since that time the resting spores have been generally regarded as zygotic in origin. Cornu and Reinsch observations were followed by the early studies of Fischer which contributed much to our knowledge of the developmental phases of these fungi. His observations and conclusions were nevertheless incorrect and confusing in several respects, and it was not until 1892 that he corrected some of his errors. Subsequent students of these olpidioid parasites, including Zopf ('84), Schröter ('86, '97), Petersen ('09, '10), Minden ('11), and others, continued to include them in the Myxochytridiales, although Lotsy ('07) and Vuillemin ('08) emphasized that the so-called chytrids with biflagellate zoospores have a different origin from those with uniflagellate zoospores and should be sharply separated from the latter. These differences were clearly recognized by Seherffel in 1925, who for the first time removed *Olpidiopsis* and similar genera from the Chytridiales and placed them at the bottom of a Saprolegniales-Peronosporales series. Seherffel's interpretation has been followed by a few mycologists, particularly Weston ('35, '41) and Sparrow ('35, '42).

In the meantime, while data about the simple olpidioid parasites were accumulating, extensive studies had been made on the more complex, elongate and mycelioid species at the other end of the series. In the group now known as the Lagenidiaceae the genera *Myzocytium* and *Lagenidium* were discovered and created by Schenk in 1858 and 1859. Because of their elongate thalli and the fact that the zoospores may be formed in a thin, extramatrical vesicle, these species were first regarded as members of the genus *Pythium* by Schenk, Pringsheim ('58, '60), and Walz ('70), although it was not then known that the zoospores are biflagellate. These workers figured and described the zoospores as uniflagellate, but the subsequent studies of Zopf ('78, '79, '84, '87) proved the presence of two flagella as well as the fact that sexual reproduction in many of the species is heterogamous. These discoveries coupled with the association of *Myzocytium* and *Lagenidium* species with *Pythium* in mycological literature emphasized their relationship to the higher filamentous Oomycetes, and the Lagenidiaceae were accordingly never included directly in the Chytridiales. Most mycologists have subsequently

incorporated this family with the Saprolegniales. Since the time of Zopf several unicellular, olpidioid species of *Myzocytium* and *Lagenidium* have been discovered, the thalli of which are strikingly similar to those of *Olpidiopsis*, so that the gap between the Olpidiidae and the elongate mycelioid members of the Lagenidiaceae has been bridged as far as thallus structure is concerned.

These simple Phycomyctes are fairly common in nature and almost world wide in distribution. So far they have been reported from Europe, Asia, and North America, and when more extensive studies are made they will doubtless be found to occur in Africa and Australia also. They are ubiquitous in host range and occur in diatoms, blue green, green, brown, and red algae, fungi, liverworts, mosses, gymnosperms, and angiosperms. Among animal hosts they have been reported in infusoria, rotifers, nematodes, weevils, mosquitoes, copepods and crustaceans. They are predominantly aquatic and may occur in marine as well as fresh water. Most species of the families Ectrogellaceae and Sirolpidiaceae parasitize marine algae. The majority of species are parasitic and eventually kill their hosts, while others are weakly parasitic or saprophytic. Obligate parasitism has been reported for a few species. They may cause marked reactions in their hosts which involve increased cell division and enlargement and lead to gall formation. Other species merely kill and absorb most of the contents of the host cells. Only one species appears to be of economic significance. *Lagena radicicola* in conjunction with other fungi causes a root disease of wheat, barley, rye, and corn which is characterized by stunted curved roots and a reduction in the root system as a whole. The stems of infected plants are considerably shorter than those of normal individuals, while the leaves may become pale-green and lighter in color and under certain conditions show "browning symptoms."

Since several of these species do not appear to be closely related, differences in types of development are to be expected, and it is impossible to give an introductory account which will apply to all families and genera. In the family Woroninaceae, as it is here interpreted, the vegetative assimilative thallus has been described as a plasmodium which undergoes cleavage at maturity. The segments thus formed may develop either into zoosporangia or resting spores. The former may be united in a sporangiosorus or lie free, and give rise to zoospores which are discharged to the outside and reinfect the host. The resting spores whenever formed usually appear as the fungus culture becomes older and more mature. In *W. polycystis* they are usually aggregated in compact cystosori as in some genera of the Plasmodiophorales, while in other species they lie loose and free. Like the sporangia, they form zoospores in germination. Neither zoosporangia nor resting spores have been observed in *Pyrrhosorus*. The spore mother cells which comprise the sorus divide three times to form eight free, thin-walled

spores, and these are soon transformed directly into zoospores, without going through a dormant period. In the polysporangiate species of *Rozellapsis* the segments of the plasmodium form either zoosporangia or resting spores, but unlike in *Woronina* they become separated by septa which the host cell forms. As a result, neither sporangia nor resting spores are united in sporangio- and cystosori, respectively. In the monosporangiate species of this genus cleavage of the thallus apparently does not occur, since each infection is reported to give rise to one zoosporangium or resting spore. In all species of the Woroninaceae, however, the zoospores encyst temporarily on the surface of the host and form during germination a penetration tube through which the spore content passes into the host cell as a naked protoplast. Nevertheless, marked differences in type of development occur in this provisional family which clearly indicate that the generic and family concepts are inadequate. The resting spores in all three genera appear to be asexual, since no fusion of gametes has been observed during their formation.

In the second family, Ectrogellaceae, no plasmodium occurs, and each zoospore gives rise to one zoosporangium or resting spore. The zoospores of this family, however, exhibit true diplanetism like those of *Achlya* and other genera of the Saprolegniales. Resting spores are known in only two species of this family. In *E. perforans* they are asexual or possibly parthenogenetic, while in *E. Licomophorae* they have been reported to be zygotic by Seherffel ('25), but the evidence of sexuality in this species is not conclusive. The family Olpidiopsidaceae includes approximately thirty species which have the same type of vegetative development as those of the Ectrogellaceae. In some species of *Olpidiopsis* the zoospores exhibit what has been described as partial and primitive diplanetism, while in *O. Oedogoniorum* and *Pythiella vernalis* they are typically diplanetie. Well defined sexuality occurs in a large number of members of this family. At the close of the vegetative period in *Olpidiopsis* fusion between thalli of unequal, and rarely of equal, size occurs which results in the formation of a thick-walled zygote. These thalli are generally described as oogonia and antheridia on the basis of relative size, but they are not markedly differentiated as gametangia or gametes. Nonetheless, the evolution and differentiation of such gametangia and heterogamy are foreshadowed in *Olpidiopsis*. The degree of sexuality varies considerably in this genus. Some species are wholly sexual or parthenogenetic while others are partially so and form only a few zygotes. In *Pythiella* an egg cell or oosphere with a trace of periplasm is formed in the oogonium—apparently an advance in heterogamy toward the *Pythium* type. So far as is now known, the development of the thallus in the Siroplidiaceae is similar to that of the Ectrogellaceae and Olpidiopsidaceae with the exception that it may become more elongate and filamentous and undergo segmentation. The segments

thus formed may separate and are transformed directly into olpidioid zoosporangia. The occurrence of resting spores is unknown or at least very doubtful in this family, and no evidence of sexuality has been reported.

In the family Lagenidiaceae the content of the zoospore does not enter the host as a naked amoeboid body, but the tip of the germ tube elongates, enlarges, and eventually develops into the mature thallus. In the majority of species the thallus is elongate, septate, and may become distinctly mycelioid. Reduced unicellular, olpidioid thalli, however, are not uncommon. In some species the segments of the thallus may separate as in the Siroplidiaceae. The segments are transformed either into zoosporangia or gametangia and both types of reproductive structures may be intermingled in the same thallus. The zoospores may be fully developed in the zoosporangia and swim directly away after emerging or are only partly formed in sporangia and undergo further development in an extramatrical vesicle. In other species the content of the sporangium emerges to the outside as a naked protoplasmic mass and undergoes cleavage into zoospores in much the same manner as in *Pythium*. The presence of a vesicular membrane around the protoplasmic mass and the zoospores which are subsequently formed has been reported in a number of species but appears to be lacking in others. In some species the zoospores encyst in a mass at the mouth of the exit tube and exhibit marked diplanetism. Sexual reproduction in this family is predominantly heterogamous, but in *Lagenidium sacculoides*, *Lagena radicicola*, and *Resticularia nodosa* it is reported to be isogamous. The segments of elongate thalli as well as entire reduced unicellular thalli which function as gametangia are only slightly or not at all differentiated as sexual organs. The female gametangium or oogonium, however, is usually larger, more vesicular, and frequently barrel-shaped, while the so-called antheridium is usually elongate and tubular. Differentiation of an egg cell and periplasm in the female gametangium has not been conclusively demonstrated, but the ooplasm may contract and aggregate toward the conjugation tube or pore during plasmogamy. The zygote which results from fusion lies free in the oogonium and is generally referred to in the literature as an oospore. In some species the antheridium is lacking, and the resting spores are formed parthenogenetically.

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## Chapter II

### Woroninaceae

Minden, 1911. Krypt. Fl. Mark Brandenburg 5: 224.

THIS FAMILY was proposed by Minden for all simple holocarpic species, exclusive of the Lagenidiaceae, which had been reported to have biflagellate zoospores, and as such it included *Olpidiopsis*, *Pseudolpidium*, *Woronina*, and *Rozella*. Minden placed this family in the Chytridiales, and together with the Olpidiaceae and Synchytriaceae it comprised the so-called Myxochytridiales of Fischer. In creating the Woroninaceae, Minden ignored Petersen's ('09) earlier-named family Pseudolpidiaceae which was proposed for *Olpidiopsis* and *Pseudolpidium*. Since Minden's time numerous other genera have been added to the Woroninaceae, and this family has been rather generally regarded as a convenient dumping ground in the Chytridiales for fungi of this type with biflagellate zoospores, although Petersen and Scherffel in particular emphasized the similarity and relationships of such fungi to the Lagenidiales and Saprolegniales. Sparrow ('42) discarded the family name Woroninaceae entirely, presumably because he believed that the genus *Woronina*, after which the family takes its name, belongs in the Plasmodiophorales. While the data at hand favor the view that *W. polycystis*, at least, is a member of this order, further intensive study of *Woronina* is needed before this question can be settled. Until this relationship is established, the present author is temporarily retaining the Woroninaceae in a restricted sense for *Woronina*, *Pyrrhosorus* and *Rozellopsis*. By this interpretation it is not, however, to be regarded as a well established and unquestionable family of closely related genera, but still as a convenient catch-all for species which are reported to have a plasmoidal vegetative stage but which at present cannot be definitely included in the Plasmodiophorales. In *Woronina*, *Pyrrhosorus*, and the septigenous species of *Rozellopsis* the plasmodium is reported to undergo segmentation into a number of closely aggregated or loose and separate spores, spore mother cells, sporangia, or resting spores, and

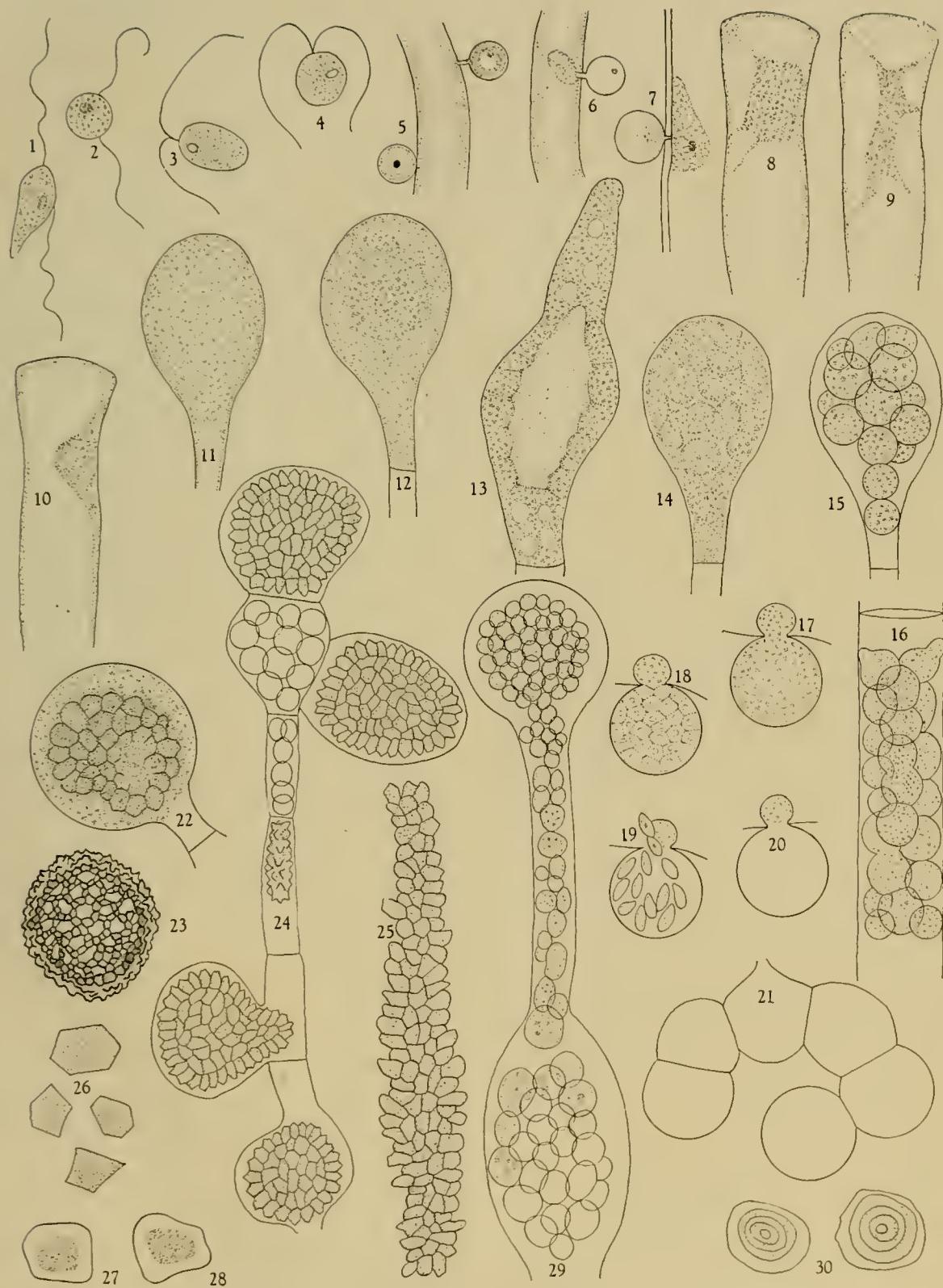
the suggestion is obvious that such species may possibly be transition forms between the Plasmodiophorales and the non-plasmoidal, non-soric genera. However, our knowledge relative to both groups is

#### PLATE 1

##### *Woronina polycystis*

- Figs. 1, 2. Biflagellate zoospores. Fischer, '82.  
 Figs. 3, 4. Anteriorly biflagellate zoospores. Cook and Nicholson, '33.  
 Figs. 5, 6. Early infection stages. Fischer, l.c.  
 Fig. 7. Same. Cook and Nicholson, l.c.  
 Figs. 8-10. Amoeboid changes in shape and position of young parasite in host cell. Fischer, l.c.  
 Figs. 11, 12, 13, 15. Successive stages in development of the parasite and its cleavage into a sporangiosorus. Note local hypertrophy and septation of host hypha. Fischer, l.c.  
 Fig. 14. Vacuolate thallus undergoing centrifugal cleavage. Fischer, l.c.  
 Fig. 16. Sporangiosorus. Cornu, '72.  
 Figs. 17-20. Maturation, cleavage, and emission of zoospores from a sporangium. Fischer, l.c.  
 Fig. 21. Small empty sporangiosorus. Cornu, l.c.  
 Fig. 22. Cleavage of thallus into a cystosorus. Fischer, l.c.  
 Fig. 23. Mature cystosorus. Cornu, l.c.  
 Fig. 24. Septate, locally hypertrophied hypha of *Saprolegnia* with five cystosori of various sizes and shapes and two empty sporangiosori. Fischer, l.c.  
 Fig. 25. Elongate, irregular cystosorus. Cook and Nicholson, l.c.  
 Fig. 26. Variously-shaped resting spores from a cystosorus. Fischer, l.c.  
 Figs. 27, 28. Thick-walled resting spores. Cook and Nicholson, l.c.  
 Fig. 29. Germination of cystosorus. Resting spores swelling and vesiculating to become zoosporangia. Fischer, l.c.  
 Fig. 30. Germination of resting spores. Cook and Nicholson, l.c.

## PLATE 1



Woronina polycystis

so incomplete at present that this suggested relationship is largely hypothetical.

## WORONINA

Cornu, 1872. Ann. Sci. Nat. 5 ser. 15: 176.

(PLATES 1 AND 2)

Thallus intramatrical, plasmodial, naked but immissible with the host protoplasm; cleaving into segments which become zoosporangia or resting spores. Zoosporangia and resting spores united in compact sporangiosori and cystosori respectively, or lying loose and free of each other. Zoosporangia usually spherical, oval or ellipsoid with a short exit papilla or an elongate cylindrical and basally inflated exit tube. Zoospore pyriform or somewhat kidney-shaped with one to several refractive granules, heterocont (?); emerging singly and fully formed; occasionally liberated within the host cell; swimming directly away in a comparatively slow and even manner. Resting spores spherical, oval, irregular and polygonal, with a smooth, spiny or sculptured outer wall; producing one or several zoospores directly in germination.

This genus has been fully discussed by the writer ('42) in relation to the phylogeny and relationships of the Plasmodiophorales. It includes at present five species most of which are incompletely known and very doubtful, and in light of present-day knowledge *Woronina* appears to be scarcely more than a dumping ground for species with a plasmodial stage which cannot be incorporated with certainty at present in the Plasmodiophorales or Proteomyxa. The type species, *W. polycystis*, has a life cycle almost identical to that of *Octomyxa* of the Plasmodiophoraceac, while *W. glomerata* resembles species of the zoosporic Myxozoidia or Proteomyxa by its animal type of nutrition. As a consequence these two species have been included in the Plasmodiophorales (Sparrow, '42) and the Proteomyxa (Zopf, '94; Scherffel, '25) respectively. The other species, *W. aggregata*, *W. elegans*, and *W. asterina*, are so imperfectly known that it is impossible to determine their taxonomic and generic distinctions. *Woronina* must accordingly be interpreted for the time being as a incoherent and questionable group of species. It is nonetheless phylogenetically significant, because it includes organisms which appear to be transitional forms between the Proteomyxa, Plasmodiophorales, and simple, holocarpic biflagellate oomycete-like fungi. Numerous undiscovered *Woronina*-like species doubtless exist, the discovery of which may possibly bridge the present-day gaps.

Sparrow ('42) disposed of *Woronina* directly by including it in the Plasmodiophorales without presenting additional evidence of its relationship to this order, but this disposition merely overlooks and does not clear up the problems involved. *Woronina polycystis* will probably prove to be a plasmodio-

phoraceous species closely related to *Octomyxa Achlyae*, and in that event some of the remaining species must be segregated in another genus. *Woronina glomerata* may well be a member of the Proteomyxa as Zopf and Scherffel contended, but further study is necessary to settle this point.

Inasmuch as these two species differ in certain respects their development will be described separately. In *W. polycystis* the contents of the zoospore enters the host hypha as a naked protoplasmic mass (Pl. 1, figs. 6-10), undergoes amoeboid changes in shape, develops into a plasmodium-like thallus as it feeds on the host protoplasm, and causes local hypertrophy (figs. 11, 12).

At maturity the thallus cleaves into segments (figs. 13, 14) which develop into zoosporangia (figs. 15, 16) and form a typical sporangiosorus. As in *Octomyxa*, the peripheral zoosporangia are usually independent with a single exit papillae, while the deeper lying ones may be confluent with a common papilla for zoospore emission. Each sporangium produces a number of biflagellate zoospores (figs. 18, 19) which reinfect the host hyphae. As the culture becomes older, the mature thalli cleave into small segments which become the resting spores. These remain closely attached and form compact cystosori of various sizes and shapes (figs. 23-25). As in *Ligniera* and *Polymyxa*, the cystosori may be elongate, irregular, flattened, oval and almost spherical, and include a few to numerous polygonal spores, each of which produces one zoospore in germination.

As to the structure of the zoospores there is, however, considerable disagreement among students of this species. Fischer described and figured them as ellipsoid (fig. 1) with a slight indentation at one side and two slightly unequal flagella. The shorter flagellum arises from the anterior end and extends forward in swimming, while the longer one is inserted laterally and projects backward. It must be noted, however, that Fischer's description was not applied directly to *W. polycystis* but related to the zoospores of *Rozella*, *Olpidiopsis*, and *Woronina* as a group. Cook and Nicholson ('33), on the other hand, described the zoospore as spherical (fig. 3, 4) with two anterior flagella which lash back and forth in breast-stroke fashion in swimming. These workers were non-committal about the relative lengths of the flagella, but most of the figures show them to be equal in length. One of their figures (fig. 3), however, shows flagella of unequal length. If the zoospores are anteriorly biflagellate, as Nicholson and Cook contended, and heterocont as Fischer reported, they do not differ fundamentally from those of the Plasmodiophorales. In view of the wide differences in observation it is not altogether improbable that what is now called *W. polycystis* may relate to more than one organism or species. Further critical studies of this species are therefore highly essential.

So far schizogony has not been reported in *W. polycystis*, and nothing is known about the type of nuclear divisions in the vegetative thallus. This parasite has never been studied critically from fixed

and stained material, and it is not improbable that future investigation may reveal the occurrence of schizogony and "primitotic" divisions. It should be noted in this connection, however, that the walls of the sporangia and resting spores of *W. polycystis* give a definite cellulose reaction, while those of the Plasmodiophorales do not. Furthermore, in germination the content of the zoospore enters the host through a penetration tube (figs. 5-7) leaving the empty case on the outside of the host cell as in *Olpidiopsis*, *Rozellopsis*, etc. In the Plasmodiophorales the zoospores are reported to enter directly. The latter difference may not be important, but the presence of cellulose is fundamentally significant, according to present-day student of phylogeny.

*Woronina glomerata* parasitizes species of *Tauheria* and causes septation of the filaments without hypertrophy (Pl. 2, fig. 1). It forms sporangio- and cystosori, but the resting spores and sporangia are not closely aggregated and compact as in *W. polycystis* but may lie loose and free of each other (figs. 6, 10, 13). Motile zoospores were observed by Tokunaga who described them as biflagellate, but nothing further is known about the number, position and relative length of the flagella. The zoospores apparently enter the host directly and divide, according to Zopf ('94, p. 54). The daughter cells soon become amoeboid and after a while may divide also (fig. 2). The amoebae feed directly on the host protoplasm and engulf starch grains, chlorophyll granules, etc., whereby they may become quite green in color. This engulfed food is held in sharply-defined vacuoles (fig. 4), according to Scherffel, and later as the cleavage segments of the plasmodium are transformed into zoosporangia or resting spores the extraneous waste material is extruded to the outside (fig. 5) like in typical proteomyxean species. As a consequence, the groups of sporangia and spores are usually accompanied by masses of dark brown waste material (figs. 1, 5, 6, 10).

The amoebae may unite by fine cytoplasmic strands or pseudopods and form a reticulate plasmodium which often completely fills the delimited portions of the host filament. The amoebae may separate again, which suggests that they do not lose their entity as cells in the large plasmodium but instead remain distinct and form a pseudoplasmodium suggestive of that in the Acrasaceae. This, however, remains to be shown. Zopf nevertheless reported that the large plasmodium cleaves into segments or "Theilplasmodien" at maturity, each of which forms a group of zoosporangia or resting spores. This division of amoebae and plasmodia is somewhat suggestive of schizogony in the Plasmodiophorales.

The resting spores, unlike those of *W. polycystis* and the Plasmodiophorales, function as zoosporangia in germination and produce numerous zoospores. The content of the spore undergoes cleavage (figs. 11, 12) into zoospore initials, while the endospore expands out through the germ pore and forms a globular vesicle which then develops a cylindrical exit tube of variable length (fig. 13A). Occasionally,

vesicles of two adjacent spores fuse and form a common one (figs. 13 B, C). After the vesicle and exit tube have been formed, the zoospores in the resting spore pass through these structures to the outside of the host. The hyaline vesicle in this species is somewhat similar in appearance to the thin-walled, hyaline zoosporangia which are developed on the surface of germinating resting spores of many chytrid species, but whether they are to be regarded as such or as inflated bases of exit tubes is not certain.

As noted above, Zopf and Scherffel regarded *W. glomerata* as an organism with a fungus-like life cycle and an animal type of nutrition, and they accordingly believed that it should be placed in the family Gymnococceaceae among the Proteomyxa.

#### W. POLCYSTIS Cornu, l.c., pl. 7, figs. 1-19.

*W. polycystis* var. *septariaformis*, Petersen, 1910, Ann. Mycol. 8:557.

Sporangiosori oval, ellipsoid, somewhat irregular or elongate,  $30 \times 100 \mu$ ,  $60 \times 476 \mu$ , often in linear rows, lying in successively delimited septate segments of the host hyphae. Zoosporangia occasionally single, usually in small or large groups, hyaline, smooth, spherical,  $12-20 \mu$ , oval, ellipsoid or polygonal with a short exit tube, or papilla. Zoospores hyaline with one small granule or globule, elongate,  $2 \times 4 \mu$ , or spherical  $3.5-4 \mu$ . Cystosori spherical, ellipsoid, barrel-shaped, cylindrical or irregular,  $42-140 \mu$ ,  $50 \times 308 \mu$ , dark brown, covered on the surface with numerous cone-shaped and pointed projections which relate to the outer cysts or spores. Individual cysts or resting spores thick-walled, spherical or polygonal,  $4-8.6 \mu$  in diameter, usually compactly united; producing one (?) zoospore in germination.

Parasitic in the vegetative filaments, zoosporangia, zoospores, antheridia and oogonia of *Saprolegnia monoica* and *S. thureti* in Germany (Fischer, '82; Minden, '11); *Achlya polyandra*, *A. racemosa*, *Achlya* sp., *Saprolegnia spiralis* and *Saprolegnia monoica* in France (Corme, l.c.; Dangeard, '90); *Achlya racemosa* in Russia (Sorokin, '83, '89); *Saprolegnia* sp., in Switzerland (Maurizio, '95); *Saprolegnia ferax*, *Saprolegnia* sp., *Achlya de Baryana*, *Achlya* sp., in England (Hartog, '90; Smith and Ramsbottom, '17; Cook and Nicholson, '33; Sparrow, '36); *Saprolegnia* sp., and *Achlya* sp., in Denmark (Petersen, '09, '10), and *Achlya* sp., in New York, U. S. A. (Sparrow, '32, '33), causing septation and marked hypertrophy of the infected filaments.

Until recently most workers regarded the parasite which Pringsheim ('60) described in *Achlya dioica* as *W. polycystis*, but Coué ('39) has shown that it relates to another species, *Pringsheimella dioica*, with posteriorly uniflagellate zoospores. Cook ('32) reported that *W. polycystis* parasitizes *Oedogonium crassusculum* var. *idiosporium* in England. This is the only account so far of its occurrence in hosts other than the water molds. The plasmodia

and sporangiosori of Cook's fungus may possibly belong to either *W. glomerata* or *W. aggregata*, or a new species. According to Fischer ('92) *W. polycystis* is limited to species of *Saprolegnia* and will not infect *Achlya*, but subsequent workers have not confirmed his observations. So far no intensive cross inoculation experiments have been made. The validity of Peterson's forma *scalariformis* is open to serious question.

As noted elsewhere, Fischer, Zopf, Cook and Nicholson described the mature vegetative thallus as a plasmodium, but they did not prove conclusively whether it arises from a single infection or by fusion of several amoebae within the host cell. Minden believed that in cases of multiple infection fusion of several protoplasts is not an improbable occurrence. According to Fischer the thallus may exhibit many of the characteristics of a plasmodium, undergoing amoeboid changes in shape which are accompanied by slow and weak wave-like streaming of its dense protoplasm. As to its mode of feeding, Zopf maintained that it engulfs the protoplasm of its host directly. Cook and Nicholson reported that it feeds on glycogen and the oil globules of its host, because they were able to demonstrate by microchemical tests the presence of the same substances in both the host and parasite. They, furthermore, maintained that the mature plasmodium or young sorus becomes surrounded by a cellulose wall as it segments into sporangia and spore rudiments; yet none of their figures show the presence of such a wall.

**W. GLOMERATA** (Cornu) Fischer, 1892. Rabenhorst's Kryptog. Fl. I, 4:64.

*Chytridium glomeratum* Cornu, l.c., p. 187, pl. 7, figs. 20-22.

Zoosporangia occasionally single, more often in small groups or loose aggregates which measure 50-96  $\mu$   $\times$  70-300  $\mu$ ; individual zoosporangia hyaline, smooth, oval or spherical, 10-33  $\mu$ , with a single broad flask-shaped exit tube which may or may not project beyond the surface of the host. Zoospores hyaline, oval, 2-2.6  $\mu$ , somewhat kidney-shaped or ellipsoid, 2.4  $\times$  3.6  $\mu$ , with numerous small granules; position and relative lengths of flagella unknown. Resting spores in groups like the zoosporangia, hyaline, spherical or ellipsoid, 12-24  $\mu$ , with a granular content, thin endospore, and thick exospore which has a net-like sculptured surface similar to that of *Tilletia tritici*; functioning as a zoosporangium in germinating and producing numerous zoospores.

Parasitic in *Vaucheria sessilis*, *V. terrestris* and *Vaucheria* sp., in France (Cornu, l.c.), Germany (Zopf, '94), Hungary (Scherffel, '25), Bulgaria (Valkanov, '31) and Japan (Tokunaga, '33), causing septation but no hypertrophy of the infected host filaments.

**W. AGGREGATA** Zopf, 1894. Physiol. Morph. Nied. Organismen 4:60.

Zoosporangia, 10 to 20 in number, grouped in round grape-like clusters or sori, hyaline, smooth

and spherical with a tubular cylindrical exit tube. Zoospores and resting spores unknown.

Parasitic in *Mougeotia* sp., in Germany.

This species has the same type of development as *W. glomerata*, according to Zopf, but differs primarily by the arrangement of the zoosporangia in the sorus and the presence of non-inflated exit tubes. Zopf also observed a similar *Woronina*-like organism in the mycelium of *Pilobolus*, but he did not identify it.

## DOUBTFUL SPECIES

**W. ELEGANS** (Perroneito) Fischer, l.c., p. 66.

*Chytridium elegans* Perroneito, 1888. Centralbl. Bakt. Parasitk. 4: 295.

Sporangesori single, spherical to star-shaped, 6-110  $\mu$ , rosy red in color and made up of 8-20 sporangia. Zoosporangia smooth, spherical, 20-30  $\mu$ , egg-shaped or pyriform with several 4-5  $\mu$   $\times$  5-100  $\mu$  cylindrical exit tubes which bore through the cuticle of the host. Zoospores oval, somewhat elongated, 2-4  $\mu$   $\times$  4-5  $\mu$ , with two long flagella and numerous minute red granules; position and relative lengths of flagella unknown. Cystosori and resting spores unknown.

Parasitic in *Phiodina rosetta* in Italy.

## PLATE 2

### *Woronina glomerata*

Fig. 1. Septate filament of *Vaucheria terrestris* with six cystosori. Zopf, '94.

Fig. 2. Septate portion of a *V. sessilis* filament with numerous amoebae, some united by fine protoplasmic strands and containing chlorophyll granules. Zopf, l.c.

Fig. 3. Same, five hours later. Amoebae have separated, begun to retract their pseudopods, and are rounding up. Extraneous chlorophyll granules have been extruded. Zopf, l.c.

Fig. 4. Two amoebae with extraneous material in food vacuoles, Scherffel, '25.

Fig. 5. Sporangiosorus of four sporangia, one of which has emitted its zoospores. Extruded waste material lying nearby. Scherffel, l.c.

Fig. 6. Large sporangiosorus. Zopf, l.c.

Fig. 7. Two large sporangiosori. Tokunaga, '33.

Fig. 8. Single sporangium undergoing cleavage. Zopf, l.c.

Fig. 9. Zoospores emerging from zoosporangia. Note inflated exit tubes. Zopf, l.c.

Fig. 10. Cystosorus of loosely united and separate resting spores. Zopf, l.c.

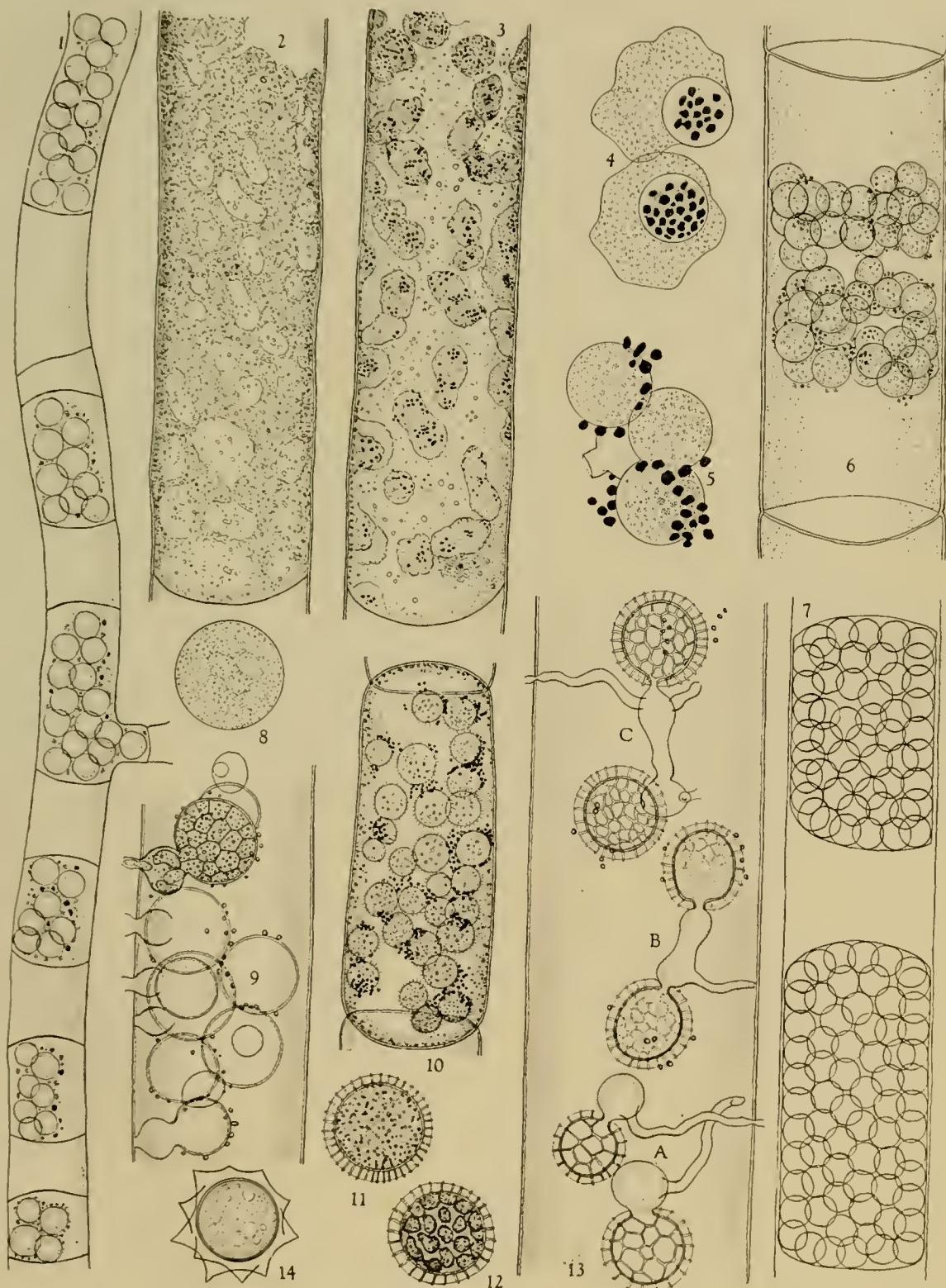
Fig. 11. Enlarged view of resting spore with sculptured exospore. Zopf, l.c.

Fig. 12. Early germination stage. Zopf, l.c.

Fig. 13. Group of germinated resting spores with long exit tubes. In two of the pairs the superficial zoosporangia or endospores have fused to form a common vesicle. Zopf, l.c.

Fig. 14. Resting spore of *W. asterina*. Tokunaga, l.c.

## PLATE 2



This species is at present a doubtful member of the genus, since the cystosori and resting spores are unknown. It differs from the other species by the presence of thick greatly elongate exit tubes on the zoosporangia.

**W. ASTERINA** Tokunaga, 1933. Trans. Saporō Nat. Hist. Soc. 13:26. Pl. 2, figs. 15, 16.

Zoosporangia 4 to 20 in number, arranged in single or double rows in delimited segments of host hyphae which measure  $18-30 \times 96-216 \mu$ ; individual zoosporangia, hyaline, smooth, spherical,  $12-19 \mu$ , opening by a small papilla. Zoospores hyaline, spherical or ovoid,  $3-4 \mu$ ; position and relative lengths of flagella unknown. Resting spores loosely aggregated in single or double rows, or lying free; hyaline, spherical,  $12-22 \mu$ , with large, broadly conical or pyramidal spines; germination unknown.

Parasitic in *Achlya americana* in Japan, causing septation by no hypertrophy of the host hyphae.

The validity of this species as a member of *Woronina* is highly questionable and the present writer is inclined to exclude it. The resting spores and sporangia are only loosely aggregated and often lie free in the segments of the host hyphae, and they may have arisen from separate individual thalli as in species of *Olpidiopsis*. Furthermore, the resting spores (fig. 14), are strikingly similar in structure and appearance to those of *O. fusiformis* (*O. minor*). Unlike species of *Olpidiopsis*, however, *W. asterina* does not cause hypertrophy of the host hyphae, but whether or not this character is specific remains to be seen.

## PYRRHOSORUS

Juel, 1901. Bih. Kgl. Svensk. Vet.-Akad. Hand.

26, afd. III, No. 14: 14.

(PLATE 3)

Thallus intramatrical, plasmoidal, naked when young but apparently immiscible with the host protoplasm; becoming invested with a wall at maturity and segmenting into spore-mother cells which aggregate to form a sorus. Spore-mother cells dividing three times to form octads of naked spores which soon become transformed into laterally biflagellate, isocont zoospores. Zoosporangia and resting spores lacking (?) or unknown.

This genus was created for an orange-colored fungus which Juel found parasitizing a red alga, *Cystoclonium purpurascens*, in Sweden. As has been pointed out by the writer ('42) in his book on the Plasmodiophorales, it has many characteristics in common with these organisms, but differs by its laterally biflagellate isocont zoospores, naked spore-mother cells and spores; lack of zoosporangia and resting spores; and by its saprophytic habit of life. As is shown in figure 1 its zoospores are strikingly

similar to those of many of the simple holocarpic biflagellate isocont Oomycete-like fungi, and off-hand it might be regarded as a transition form between this group and the Plasmodiophorales. However, to interpret it as such does not seem fully warranted at present, since the complete life cycle of *P. marinus* apparently is not known. For the time being, *Pyrrhosorus* is included in the Woroninaceae as this family is herewith interpreted.

**P. MARINUS** Juel, l.c., p. 14, figs. 1-29.

Plasmodium or thallus partly or completely filling host cell and extending into adjacent cells. Spore-mother cells spherical,  $8 \mu$ , with numerous refringent orange globules. Zoospores pyriform,  $2.5 \times 4.5 \mu$ , with an orange pigment spot; flagella oppositely directed in swimming.

Saprophytic in dead branches of *Cystoclonium purpurascens* in Sweden.

The life cycle of *P. marinus* is as follows: In the early developmental stages it consists of small globular thallus lying within the host cell (fig. 2). Such thalli may often be associated in pairs (fig. 3) or groups, and Juel accordingly considered it possible that they may later coalesce and form a large plasmodium. The uninucleate thallus grows in size as its nucleus enlarges (fig. 4) and apparently divides. Mitoses in the plasmodium have not been observed, and Juel was uncertain as to the manner of origin of the multinucleate stages. A later stage is shown in figure 5 of a plasmodium with four large nuclei. The developing plasmodia apparently have the ability to dissolve intervening cell walls (fig. 5) and may eventually occupy several cells. Although they may be distinctly amoeboid in shape with numerous blunt

## PLATE 3

### *Pyrrhosorus marinus*

(All figures after Juel)

Fig. 1. Laterally biflagellate isocont zoospores with an orange colored eye spot.

Fig. 2. Uninucleate thallus.

Fig. 3. Paired young thalli.

Fig. 4. Uninucleate thallus with enlarged primary nucleus.

Fig. 5. Four-nucleate thallus passing through cell wall.

Fig. 6. Multinucleate thallus.

Fig. 7. Multinucleate amoeboid thallus.

Fig. 8. Cleavage into spore-mother cells.

Fig. 9. Sorus of spore-mother cells.

Fig. 10. Isolated spore-mother cell.

Fig. 11. A sorus, the spore-mother cells of which have divided into groups of four daughter cells.

Fig. 12. Spindle-shaped spore-mother cells (?) in a branched thallus.

Fig. 13. Spindle-shaped spore-mother cells and accessory sterile cells in an elongate host cell.

Fig. 14. Sorus with spore-mother and sterile cells.

Fig. 15. Nuclei of spore-mother cells dividing.

Fig. 16 to 19. Mitosis and cytokinesis of spore-mother cells.

## PLATE 3



Pyrrhosorus

pseudopod-like extensions and vacuoles (figs. 6, 7) it is not certain from Juel's account that they move about and migrate from cell to cell as in *Plasmodiophora*, etc. No evidence of schizogony was observed by Juel, but Winge interpreted some of the uninucleate stages as probable meronts.

The mature plasmodium is multinucleate, vacuolate, and usually irregular in shape (figs. 6-8), and just before sporulating forms an enveloping membrane like *Sorolpidium*. Plasmodia which are extensively drawn out and occupy several host cells may accordingly appear lobed, irregular, and tubular (fig. 12) after the wall has formed. Following this stage the protoplasm divides into uninucleate segments. In this process no distinct cleavage furrows have been observed. The plasmodium appears to become highly vacuolate (fig. 8) during this process, and the cytoplasm accumulates around the nuclei and forms stellate protoplasmic islands which resemble somewhat the sporonts of *Tetramyxa*. These segments soon become almost spherical or spindle-shaped (fig. 12), and Juel thought that the latter type of cells are formed in plasmodia which are highly vacuolate and scarce in cytoplasm. In addition to these two kinds of segments, irregular elongate, oval and smaller ones may be formed, apparently as the result of unequal cleavage, which finally degenerate.

The spherical, 8  $\mu$  in diameter, and spindle-shaped segments are uninucleate, naked, and never develop a distinct wall. They aggregate to form a definite sorus (fig. 9) and each cell soon divides into octads of spores as in *Octomyxa*, which led Juel to call them spore-mother cells. In this process of spore formation the nuclei divide mitotically (figs. 15-18) and each mitosis is followed by cell division. Definite chromosomes (2 to 5) are formed on a sharply-defined spindle during mitosis, and there is no evidence of "promitosis," according to Juel's figures. Each of the eight naked spores soon becomes transformed directly into zoospores without developing thick walls and becoming dormant. The zoospores apparently infect the host cells and develop into the small thalli shown in figures 2 and 3.

## ROZELLOPSIS

Karling, 1942. Amer. Jour. Bot. 29: 33. Mycologia 34: 205.

(PLATE 4)

Thallus, intramatrical, more or less indistinguishable from but apparently immiscible with the host protoplasm; becoming invested with a wall at maturity and forming one sporangium; or cleaving (?) into several segments which become separated by host walls, mature in basipetal succession, and develop into sporangia or resting spores. Sporangia terminal or intercalary in host hyphae, variable in size and shape, with one to several exit papillae

which extend through the host wall; usually filling the host sporangia or the hypertrophied portions of the hyphae completely; sporangium wall tightly pressed against, seemingly fused with, and usually indistinguishable from that of the host. Zoospores slightly variable in size and shape, with one to several minute globules, heterocont, shorter flagellum usually extending forward and the longer one backward in swimming; zoospores swirling in the sporangium before emerging and swimming away; content of zoospore flowing into host cell through an infection tube in germination, leaving the empty zoospore case attached to host cell. Resting spores unknown in monosporangiate species; solitary in septigenous polysporangiate species, lying free within host cell and separate from host wall, variable in size, brown and spiny; protoplasm coarsely granular, including a large vacuole or globule of hyaline material; germination unknown.

This genus was created for the *Rozella*-like species with biflagellate heterocont zoospores which have been described from time to time. As such it is perhaps scarcely more than a provisional dumping ground for imperfectly known species of this type. It was proposed primarily to include *Pleolpidium inflatum* Butler ('07) and a similar parasite which Miss Waterhouse ('40) found in *Phytophthora*. Whether or not the species which Fischer described as *R. septigena* and *R. simulans* belong here is obviously open to question. He figured and described the zoospores as biflagellate and heterocont, but it is particularly noted in this connection that his description does not apply specifically to these species. It relates instead to the zoospores of *Woronina*, *Olpidiopsis* and *Rozella* collectively. Inasmuch as many of Fischer's observations of other similar parasites have proven inaccurate, it is not altogether improbable that he may have been mistaken about the number, relative lengths, and position of the flagella. On the other hand, it is equally probable that he had at hand a different fungus from the one described by Cornu as *R. septigena*. This is suggested by Tokunaga's ('33) confirmation of Fischer's report of biflagellate heterocont zoospores in *R. simulans*, which is identical to *R. septigena* except in host range. For this reason Fischer's *R. septigena* has been separated from Cornu's species of the same name and placed temporarily with *R. simulans* in *Rozellopsis*. This genus accordingly includes two incompletely known aseptigenous monosporangiate, and two doubtful septigenous, polysporangiate species.

So far as is now known *Rozellopsis* has the same type of development as *Rozella*. In monosporangiate species the thallus develops into one sporangium or resting spore, whereas in the septigenous members the thallus is reported to segment into several portions, each of which develops into a sporangium or a spore. Germination of the zoospores, infection, and entrance of the parasite have not been observed in *R. inflata*, so that the following description of the processes is based on *R. waterhouseii* and *R. septi-*

gena. According to Fischer and Miss Waterhouse the zoospores come to rest on the host hyphae and develop germ tubes of variable lengths (figs. 5-7, 16) which penetrate the host wall. The contents flow into the fungus hyphae through this tube and soon become obscured by and almost completely lost to sight in the host protoplasm. Although it is not visible as a clearly-defined body its presence is nevertheless evident by the increased density and opacity of the host protoplasm in the region of infection. Fischer reported that the young thallus of *R. septigena* loses all individuality as it mixes with the host protoplasm and develops into a plasmodium, but his account is not based on observations of fixed and stained material. It is not improbable that the parasite remains naked until very late in development, but it is apparently imminiscible with the host protoplasm. If it is amoeboid in shape with numerous fine pseudopods it may well infiltrate the interstices of the host protoplasm and appear to be fused or mixed with the latter. This, however, remains to be determined by intensive cytological study of fixed and stained material.

As the parasite increases in size and attains vegetative maturity, numerous small vacuoles usually appear in the cytoplasm of the hypertrophied portions of the host hyphae (figs. 9, 16), but it is not always certain whether these vacuoles relate to the cytoplasm of the parasite or the host. However, since they seem to fuse later and form the large central vacuole of the parasite's sporangium (fig. 10) they probably relate to the parasite. Such vacuoles may move about and undergo marked changes in shape from time to time (fig. 9). According to Butler, the vacuolate stage is not very marked in *R. inflata*. At this stage one or more dome-shaped exit papillae are usually present which project through the host wall (figs. 9, 10). Their presence is probably an indication that the parasite has reached vegetative maturity and been transformed into an incipient sporangium. The formation of the sporangium wall has never been observed, but it has been described in the literature as indistinguishable from and seemingly fused with that of the host. However, by plasmolytic experiments Miss Waterhouse demonstrated that *R. waterhouseii* has a distinct membrane of its own which may be readily separated from the host wall. Whether or not it is composed largely of cellulose had not been determined.

Cytokinesis is probably accomplished by centrifugal cleavage furrows which progress from the border of the central vacuole to the periphery, although it has not yet been clearly demonstrated. According to Miss Waterhouse, the visible changes in the protoplasm preparatory to sporogenesis are quite characteristic. The central vacuole may disappear, leaving the protoplasm quite clear and homogeneous except for a few dark granules in the center. Shortly thereafter the protoplasm takes on the appearance as if it had undergone cleavage into zoospore initials, but this phase persists only for a short time. The

protoplasm becomes optically clear again, and after a period of about half an hour the exit papillae de-liquesce and disappear completely, leaving a cytoplasmic membrane across the orifice. Following this stage the protoplasm becomes finely reticulate in appearance, and shortly thereafter the definitive spore initials are formed (fig. 11). As these become more clearly defined the whole mass of segments begins to glide and move around. This movement increases in intensity until the zoospores are swarming and swirling around in the sporangium. Within a few minutes the membrane across the orifice bursts and the zoospores are discharged in a dense cloud-like mass.

All species of *Rozellopsis* are reported to have heterocont zoospores with the shorter flagellum extending forward in swimming (figs. 4, 13, 15). The exact point of insertion of the flagella is not certain in *R. waterhouseii*, but in *R. inflata* and *R. septigena* Fischer and Butler reported that the short flagellum arises from the anterior end (fig. 15) while the longer one is laterally inserted. In *R. simulans*, on the other hand, both flagella arise from the anterior end (fig. 23) as in the Plasmodiophorales, according to Tokunaga. In swimming the zoospores move along more evenly and smoothly in a straight or curved path in marked contrast to the jerky darting motion of the zoospores of *Rozella* species. They may also round up and encyst (fig. 14), but so far no evidence of diplanetism has been observed.

The development of septigenous species is similar to that described above for aseptigenous members, with the exception that the thallus produces more than one sporangium or resting spore. Fischer described the thallus in *R. septigena* and *R. simulans* as a plasmodium which fragments or undergoes schizogony into several segments. Although he frequently noted instances of multiple infection (fig. 16) Fischer nonetheless believed that each plasmodium is the product of a single infection. As evidence that the thallus fragments, he reported cases of single spores giving rise to 5, 2, 4, and 7 sporangia. In cases of multiple infection the resultant thalli or plasmodia remain separate and do not fuse, according to Fischer. As noted elsewhere his studies do not relate to experimentally controlled monosporic infections, and until such studies have been made the problem of whether or not a single infection eventually gives rise to several sporangia or resting spores remains to be conclusively settled. However formed, the thallus or plasmodium is reported to fragment and the portions become separated by transverse host walls and mature in basipetal succession (figs. 17, 22).

The process of resting spore formation in the septigenous species appears to be the same as that of *Rozella*, although it must be noted in this connection that Fischer's figures (figs. 18-21) may possibly relate to *Rozella* instead of *Rozellopsis*. Assuming that the stages shown in figures 18 to 21 belong to the parasite with biflagellate heterocont zoospores (fig. 15), it is evident that the process is strikingly

similar to that of *Rozella*. The portions of the thallus or "plasmodium" in the hypertrophied hyphal segments or swollen side branches appear to contract and become invested with a wall (fig. 19), so that they lie loose and free in the host cell. The incipient spores usually lie in a clear space which in turn is surrounded by a layer of host cytoplasm (fig. 20) from which strands radiate to the periphery. The clear area is apparently the region in which the host cytoplasm is transformed into spore wall material, because as the cytoplasm decreases in amount definite spines are deposited on the outer wall of the spore (figs. 20, 21). The spines and echinulations seem thus to be nothing more than modified host protoplasm as Butler ('07) and McLarty ('41) have shown in *Olpidiopsis Pythii* and *O. Achlyae*. Germination of the resting spores has not been observed, but they probably give rise directly to zoospores as in *Rozella*.

As is shown in plate 4, *Rozellopsis* produces a marked reaction in the host hyphae which involves both cell enlargement and cell division. Hypertrophy is local and confined largely to the region of infection. According to Miss Waterhouse's figures (figs. 5-7) it may even begin during infection. Eventually the infected portions of the hyphae may become ten to fifteen times their normal diameter (figs. 1-3) and are usually delimited from the remainder of the mycelium by cross walls (figs. 9-12, 16, 17, 22). Such cross septa may become unusually thick (figs. 11, 12) and in extreme cases project up or down into the hypertrophied portions as dome-shaped plugs. In the cases of infection by septigenous species the fragments of the "plasmodium" are successively delimited by walls, so that an infected hyphal tip may have a large number of cross septa (figs. 17, 22). The reaction of the host nuclei and cytoplasm to the presence of the parasite is not known, since most studies to date have been made on living material. However, as noted previously, Fischer believed that the two protoplasts mix and become indistinguishable, but this seems unlikely.

The taxonomic position and relationship of *Rozellopsis* to the simple holocarpic biflagellate fungi are very uncertain at present, and solution of these questions must await further study. In view of the reports that its thallus is a plasmodium which undergoes schizogony in the septigenous species, *Rozellopsis* is herewith included provisionally in the family Woroninaceae in the restricted sense noted above. This disposition is obviously temporary and may be completely invalidated by future studies. The presence of a plasmodium which may undergo fragmentation still remains to be demonstrated in *Rozellopsis*, in the writer's opinion. If schizogony does occur in the septigenous members it may become necessary to segregate them in a separate genus. The presence of anteriorly biflagellate heterocont zoospores in *R. simulaans* suggests direct affinity with the Plasmodiophorales, but this relationship likewise remains to be proven.

### Aseptogenous Monosporangiate Species

**R. INFLATA** (Butler) Karling, 1942. Amer. Jour. Bot. 29:34.

*Pleolpidium inflatum* Butler, 1907. Mem. Dept. Agric. India. Bot. ser. 1: 126, 127, pl. 7, figs. 17-21.

Sporangia terminal, spheroidal, up to 85  $\mu$  in diameter, oval, or pyriform with one to several exit papillae. Zoospores reniform, kidney-shaped with the shorter flagellum attached at the anterior end and the longer one at the side; swimming smoothly in long curves. Resting spores unknown.

Parasitic in *Phytium intermedium*, Antibes, France, causing marked hypertrophy of the host sporangia.

**R. WATERHOUSEII** Karling, l.c., p. 34.

Sporangia terminal, spherical, up to 74  $\mu$  in diameter, clavate, oval, or obpyriform with 1-3 apical or lateral exit papillae. Zoospores pyriform, 5-8  $\mu$

### PLATE 4

#### *Rozellopsis inflata*

(Figs. 1-4 after Butler, '07; figs. 5-14 after Miss Waterhouse, '40; figs. 15-21 after Fischer, '82; figs. 22, 23 after Tokunaga, '33.)

Fig. 1. Sporangia in the hyphal tips of *Pythium intermedium*.

Fig. 2. Zoospores within a sporangium.

Fig. 3. Empty sporangium.

Fig. 4. Heterocont zoospores with one or two refractive globules at the ends.

#### *R. waterhouseii*

Figs. 5-7. Infection of hyphal tip of *Phytophthora cryptogaea*.

Fig. 8. Early stage of hypertrophy.

Fig. 9. Later stage. Sporangium of parasite delimited by cross septa, multivacuolate with one exit papilla.

Fig. 10. Still later stage in which the vacuoles have fused to form a large central one.

Fig. 11. Sporangium with zoospore initials.

Fig. 12. Zoospores swarming in the sporangium and emerging through the exit orifice.

Figs. 13, 14. Heterocont motile, and encysted zoospores.

#### *R. septigena*

Fig. 15. Heterocont zoospores with one refractive globule. Shorter flagellum at anterior end.

Fig. 16. Multiple infection of *Saprolegnia* hyphal tip.

Fig. 17. Hypertrophied and septate host hypha with several "Reihensporangien" in various stages of development.

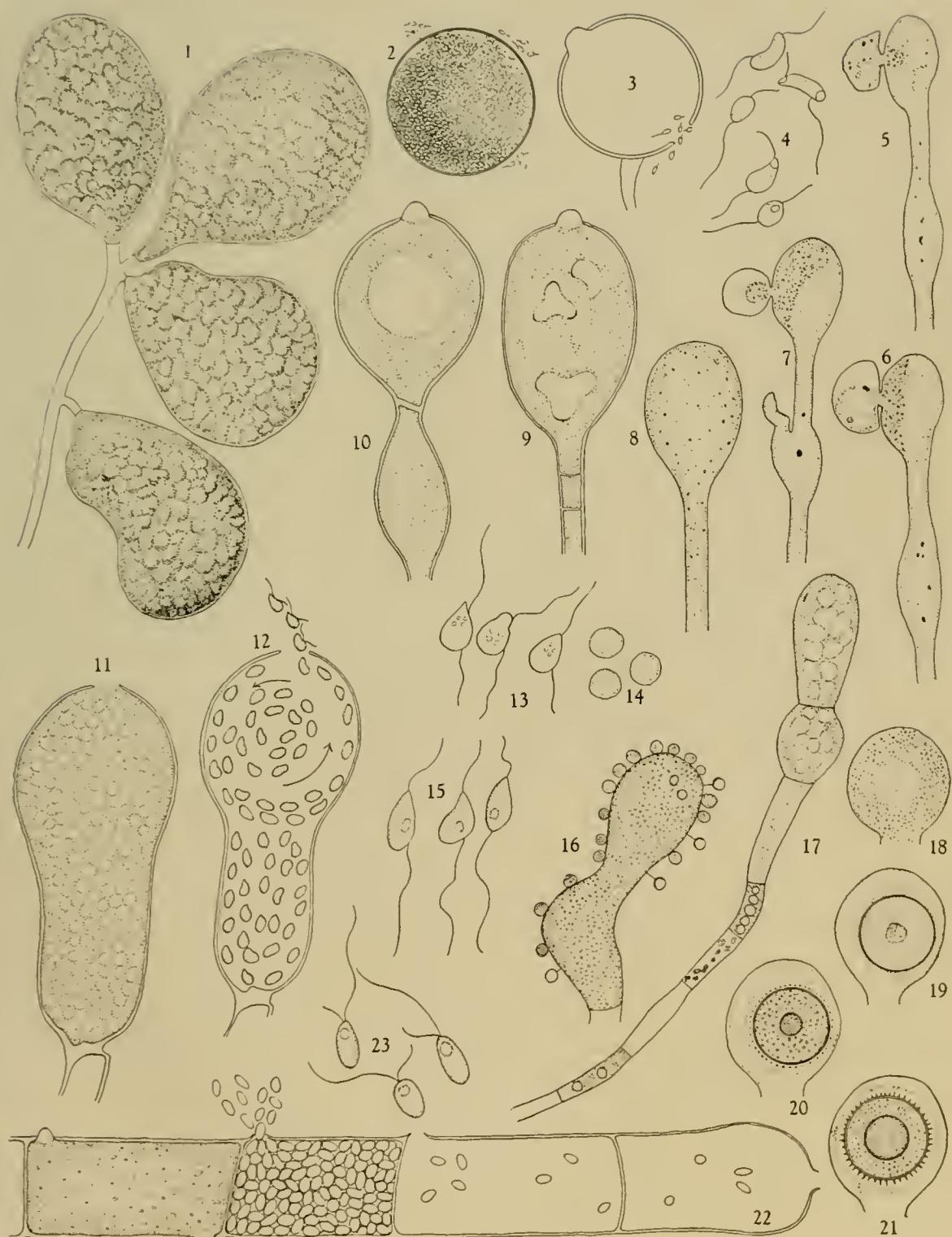
Figs. 18-21. Stages in development of the resting spores.

#### *R. simulaans*

Fig. 22. Infected hypha of *Achlya flagellata* with sporangia in various stages of maturity.

Fig. 23. Anteriorly biflagellate heterocont zoospores with a refractive globule.

## PLATE 4



Rozellopsis

long with a few small refringent granules in the center or near the posterior end; flagella apparently laterally inserted (?); zoospores active for twenty-four hours or more, or rounding up and encysting. Resting spores unknown.

Parasitic in *Phytophthora cryptogaea* and *P. megasperma*, London, England, causing occasional hypertrophy of the host sporangia and supporting hyphae.

Miss Waterhouse discovered this parasite in material collected from the Hogsmill River, a Surrey tributary of the Thames, and gave an excellent account of its development and infection of the host. She succeeded in inoculating *P. megasperma* with it, but all attempts to infect *Rhipidium continum* and *R. americanum* were unsuccessful. This species differs from *R. inflata* by its pyriform zoospores and the fact that it causes only slight hypertrophy of the host. Because of its similarity in other respects to Butler's species, Miss Waterhouse, however, did not diagnose it as a new species.

### Septigenous Polysporangiate Species

#### **R. SEPTIGENA** (Fischer) Karling, I.c., p. 34.

*Rozella septigena* Fischer, 1882. Jahrb. wiss. Bot. 13:321. Pl. 14, fig. 19; pl. 15. (Not *R. septigena* Cornu, 1872.)

Sporangia up to 20 in a linear row in delimited segments of the host hyphae, of the same size and shape as the hyphal segments, with 1-2 apical or lateral exit papillae. Zoospores elongately pyriform,  $2.4 \mu \times 6-8 \mu$ , hyaline, with a minute central refractive spot; shorter flagellum anteriorly attached, longer flagellum lateral. Resting spores solitary in segments of the hyphae or in short swollen side branches or "false oogonia," spherical,  $20 \mu$ , with a hyaline endospore and spiny brown exospore, spines  $2 \mu$  long; contents coarsely granular, including a large refractive globule; germination unknown.

Parasitic in *Saprolegnia monoica* and *S. thureti* in Germany (Fischer, I.c.; Minden, I.c.) causing hypertrophy and septation of the host hyphae.

Fischer's attempts to inoculate *Achlya* with this species failed, and he accordingly concluded that it is limited in host range to *Saprolegnia*. His results have not been confirmed experimentally.

#### **R. SIMULANS** (Fischer) Karling, I.c., p. 34.

*Rozella simulans* Fischer, I.c., p. 321; Minden, I.c., p. 271, fig. 11a; Tokunaga, 1933. Trans. Sapporo Nat. Hist. Soc. 13:25. Pl. 2, figs. 12-14.

Sporangia up to 15 in a linear row in delimited segments of the host hyphae, cylindrical, barrel-shaped,  $25-90 \mu \times 60-250 \mu$ , with 1-2 apical or lateral exit papillae. Zoospores elongate, ellipsoidal,

$2.4 \mu \times 6 \mu$ , hyaline, with a small refractive spot and two unequal flagella attached at the anterior end. Resting spores solitary in short swollen side branches or "false oogonia," of the same size, shape, content, and appearance as those of the previous species; germination unknown.

Parasitic in *Achlya polyandra* and *A. racemosa* in Germany (Fischer, I.c.; Minden, I.c.), *Achlya* sp., in Switzerland (Mauricio, '95), and *A. flagellata* in Japan (Tokunaga, I.c.), causing hypertrophy and septation of the host hyphae.

According to Fischer, this species is similar to *R. septigena* and differs only by its limitation in host range to species of *Achlya*. Subsequent workers who reported its occurrence, however, did not make cross inoculations but accepted Fischer's observations without question. Inasmuch as Minden apparently did not determine the number, relative lengths, and position of the flagella of his fungus, it is just as probable that the resting spores which he figured relate to *R. septigena* as to the present species. Likewise, it is not certain that Tokunaga's species is *R. simulans*, although the host reactions and sporangia are similar. He figured the zoospores as anteriorly biflagellate and narrow, while Fischer described them as large and exactly similar to those of *R. septigena* with the short flagellum anteriorly and the long one laterally attached. Consideration, however, must be given to the difficulty of determining the exact position of the flagella on active zoospores, and it is possible that these differences in observations are due to this factor. If this species is identical to *R. septigena*, as Fischer maintained, and will infect only *Achlya*, it may possibly be a physiological race of the former species.

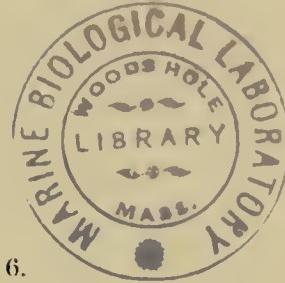
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## Chapter III

## Ectrogellaceae

Scherffel, 1925. Arch. Prolistk. 52: 6.



THIS FAMILY supercedes the Eurychasmaceae which Petersen created in 1905 for the genus *Eurychasma*. Because Petersen included his family in the Myxochytridiales, with which it has little in common except for its olpidioid holocarpic thalli, Scherffel regarded the Eurychasmaceae as invalid. Although he placed *Eurychasma* and *Ectrogella* in the Saprolegniaceae, he nevertheless suggested (p. 6) that they might comprise a separate family, the Ectrogellaceae, which he described as a group of simple saprolegniaceous fungi the thalli of which are transformed holocarpically into single zoosporangia. Coker and Matthews ('37) incorporated Scherffel's family in the Saprolegniales and added the genus *Aphanomyopsis* which Scherffel had included in the Saprolegniaceae. A similar interpretation was made by Sparrow in 1933 and 1936. In his recent ('42) classification of the aquatic Phycomycetes he placed the Ectrogellaceae as the first and most primitive family of the Saprolegniales and added his new genus *Eurychasmidium* to the group. According to his classification, this family includes *Ectrogella*, *Eurychasma*, *Eurychasmidium*, and *Aphanomyopsis*. Whether *Aphanomyopsis* belongs here or in the Lagenidiaceae or Saprolegniaceae is open to serious question. As will become more evident below its thalli may be strikingly similar to those of parthenogenetic species of *Lagenidium*. On the other hand, it may also have the appearance of a species of *Aphanomyces* in which sporangia are not well differentiated.

The suggested relationship of this family to the Saprolegniaceae is based largely on the similarity in method of zoosporogenesis, the presence of diplanetism, and in the structure and behavior of the zoospores, since evidence of sexual reproduction in the Ectrogellaceae is at present very meager and inconclusive. Resting spores are unknown in *Eurychasma*, *Eurychasmidium* and in all species of *Ectrogella* except *E. Licmophorae* and *E. perforans*. In *Aphanomyopsis* they appear to be formed parthenogenetically or merely by the contraction and encystment of the cell content. In *E. Licmophorae* fusion of undifferentiated male and female thalli has been reported, but the evidence presented is not conclusive.

## ECTROGELLA

Zopf, 1884. Nova Acta K'sl. Leop.-Carol. Deut. Akad. Nat. 47: 175.

(PLATE 5)

Thallus intramatrical, holocarpic, wall showing a more or less marked cellulose reaction when tested

with chloro-iodide of zinc; oval, elongate, cylindrical and vermiform; forcing the valves of the diatom host apart at maturity. Zoosporangia single or numerous, hyaline, smooth, oval, egg-shaped, elongate, cylindrical, vermiform and slightly irregular, sometimes becoming partially extramatrical at maturity, with one to several comparatively short, wide, tapering exit tubes which project between the separated valves of the diatom cell. Zoospores variable in shape, hyaline, with one to several small refractive granules; usually becoming active within the sporangium; diplanetic, primary swarmers anteriorly or laterally biflagellate and isocont, emerging singly and swimming directly away as in *Saprolegnia*; or aflagellate, gliding out and encysting in a group at the mouth of the exit tube as in *Achlya*; secondary swarmers oval, lemon-shaped, and pyriform, usually with a ventral furrow, laterally biflagellate with the flagella inserted nearer the anterior end; the shorter active flagellum directed forward and the longer one backward in swimming. Resting spores hyaline, smooth, spherical or oval, thick-walled with one large or several smaller refractive globules; formed parthenogenetically or by the fusion (?) of the contents of a small male thallus or antheridium (?) with that of female thallus through a broad conjugation tube; germination unknown.

This genus was first included in the Olpidiaceae, but since the discovery that the zoospores are biflagellate and diplanetic it has been regarded, particularly by Scherffel, Coker and Matthews, and Sparrow, as a primitive group of the Saprolegniales. As it is here constituted *Ectrogella* includes five species, some of which may possibly prove to be identical from future studies. All are parasites of diatoms and infect marine as well as freshwater species.

The life history and development of *Ectrogella* species are shown in plate 5. The zoospores come to rest on the host cell and put forth a germ tube which soon penetrates the silicified wall of the host (fig. 1). The content of the spore then flows into the host, leaving the empty zoospore case and penetration tube behind. The young thallus is at first uninucleate, naked and amoeboid with numerous pseudopods (fig. 28) but becomes enveloped by a thin membrane or wall very shortly after entering the host cell. Multiple infection may frequently occur, so that as many as thirty young thalli may occasionally be found in a single cell. As the thalli develop the chloroplasts of the host begin to lose their normal color, disintegrate and break down. So far no direct engulfing of masses of host protoplasm or discrete bodies by the thallus has been observed. With in-

crease in size and maturity the wall of the thallus becomes well defined and conspicuous, while the protoplasm takes on a greyish-granular appearance like that of the Saprolegniaceae (figs. 1-2). Numerous small vacuoles are usually present during the early development stages (figs. 6, 7) but these gradually fuse into a large central one with an irregular outline (figs. 10, 19). As a result the remainder of the protoplasm is displaced towards the periphery of the sporangium where it forms a comparatively thin, irregular, parietal layer. Simultaneous with these changes and the transformation of the thallus into a zoosporangium the valves of the diatom cell are spread apart (fig. 18), and the exit tubes begin the push out. These vary greatly in number, diameter, and length, and in *E. Liemophorae* become thick-walled and inflated at the base, whereby they are able to separate the valves of the diatom. As a result of this spreading apart of the diatom shell and the growth of the exit tubes, the zoosporangium may become partially extramatrical, and in *E. perforans* and *E. Liemophorae* especially, it has much the same appearance and relation to the host as that of *Eurychasma*.

The exit tubes and adjacent portions of the mature sporangium wall give a marked cellulose reaction when treated with chloro-iodide of zinc, while the remainder of the wall reacts only slightly or not at all. Petersen ('05) interpreted this difference as a matter of age and activity. Scherffel found that the empty zoospore cysts likewise give a marked cellulose reaction.

Cleavage and zoosporogenesis occur in the same manner as in the Saprolegniaceae according to Scherffel. Furrows progress centrifugally from the border of the central vacuole (figs. 10, 19, 22) and thus delimit the zoospore initials. As these furrows progress numerous small refractive globules may appear at the inner periphery of the zoospore rudiments (fig. 23). When the cleavage furrows have reached and cut through the plasma membrane, the central vacuole disappears, and the whole sporangium takes on a coarsely granular appearance and the zoospore initials are no longer visible (fig. 11). This is known as the homogeneous granular stage of zoosporogenesis. It is doubtless the result of a rehydration and swelling of the zoospore *anlagen*, as Harper ('99) described for *Synchytrium*, whereby the lines of demarkation become very faint or invisible. After some time the outlines of the zoospores become visible again (fig. 14), and shortly thereafter they begin to shake, wobble, and glide upon each other. These are the so-called primary swimmers which are oval to pyriform in shape and may be biflagellate or have two equal rudimentary flagella attached laterally (fig. 13), or at the anterior end (figs. 26, 30, 31). These primary swimmers may emerge and swim directly away as in *Saprolegnia*, or glide out and encyst at the mouth of the exit tubes as in *Achlya* (figs. 14, 27, 32).

Scherffel regarded the method of cleavage and zoosporogenesis described above as typical of the

Saprolegniaceae and not of the Chytridiales, and for this and other reasons he maintained that *Ectrogella* is a member of the former family. As the present writer has pointed out previously ('37) cleavage in this genus is not fundamentally different from that described by Harper ('99, '14), Swingle ('03), Schwarze ('22) and others for the Mycetozoa, Chytridiales, Oomycetes and Zygomycetes in general. The point which Scherffel tried to emphasize is not

## PLATE 5

### *Ectrogella bacillariacearum*

(Figs. 2-5, 17, 18 after Zopf, '84; fig. 35 after Petersen, '09; remainder after Scherffel, '25.)

- Fig. 1. Early infection of *Synedra* cell.
- Fig. 2. *Synedra* cell with 21 small parasites.
- Fig. 3. *Synedra* cell with one elongate tubular parasite.
- Fig. 4. Surface view of infected *Synedra* cell.
- Fig. 5. Mature sporangium with central vacuoles.
- Figs. 6-9. Stages of growth and maturation of sporangium. Small vacuoles fusing to form central row of larger vacuoles.
- Fig. 10. Centrifugal cleavage.
- Fig. 11. Contracted granular stage following cleavage.
- Fig. 12. Reappearance of outlines of cleavage segments.
- Fig. 13. Primary zoospores with rudimentary flagella.
- Fig. 14. *Synedra* cell with encysted *Ectrogella* zoospores at mouth of exit papillae.
- Fig. 15. Empty cysts and secondary zoospores.
- Fig. 16. Laterally biflagellate heterocont secondary zoospores.
- Figs. 17, 18. Empty zoosporangia with several exit papillae.

### *E. monostoma*

- Fig. 19. Mature zoosporangia undergoing cleavage; exit papilla at A.
- Fig. 20. Empty cysts and cystospores at mouth of exit papilla.
- Fig. 21. Laterally biflagellate heterocont secondary zoospores with a large vacuole.

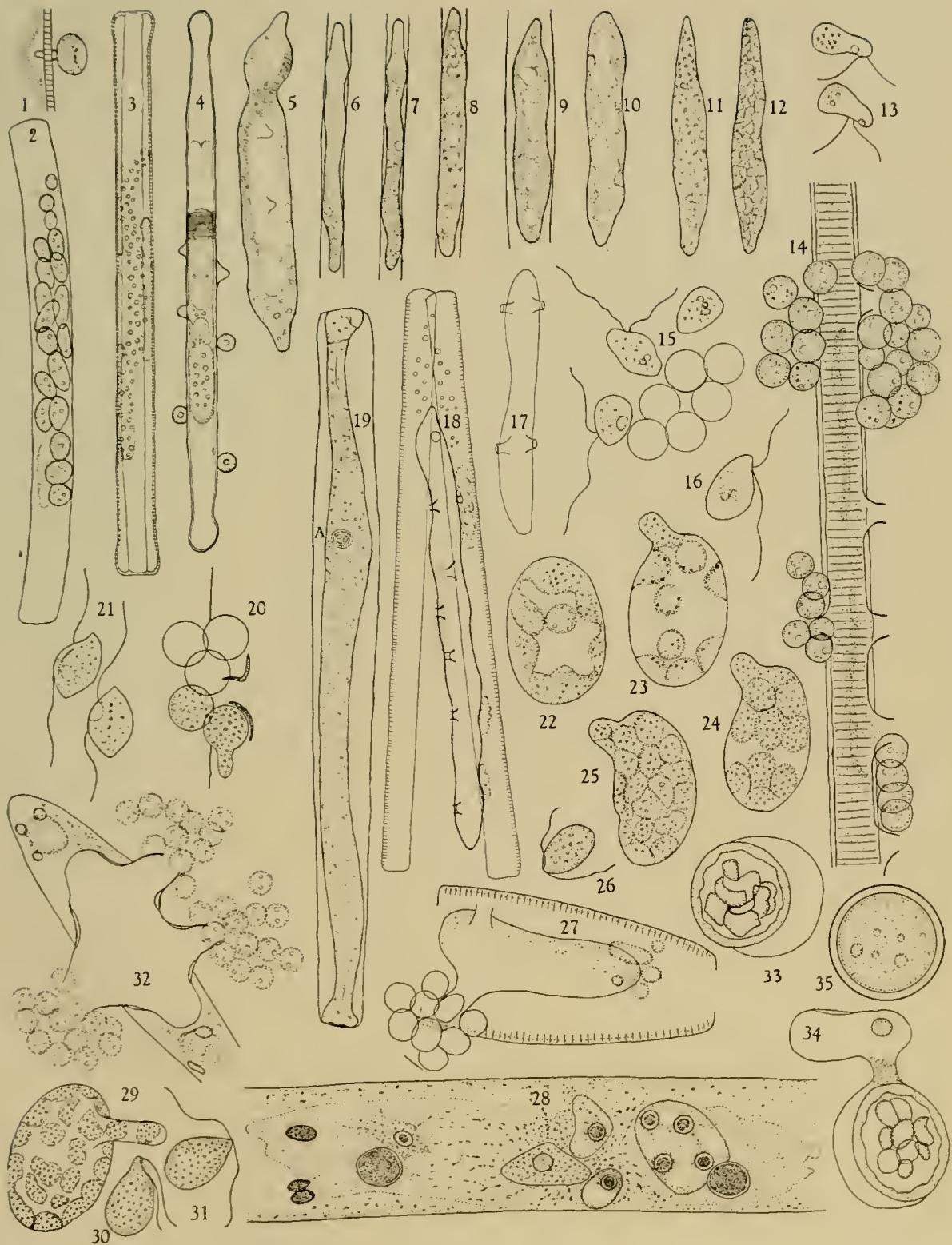
### *E. Gomphonematis*

- Figs. 22-25. Cleavage stages in a zoosporangium.
- Fig. 26. Anteriorly biflagellate primary zoospore.
- Fig. 27. Empty sporangium with two exit papillae. Zoospores encysted at one papilla, while those which emerged from other papilla swam away.

### *E. Liemophorae*

- Fig. 28. Portion of a *Liemophora* cell showing a naked amoeboid uninucleate thallus with pseudopods at left; two uninucleate thalli with walls near host nucleus in center; and a tetranucleate thallus at right.
- Fig. 29. Mature sporangium with cleavage segments.
- Figs. 30, 31. Anteriorly biflagellate primary zoospores.
- Fig. 32. Zoospores encysted at mouth of exit papillae.
- Fig. 33. Parthenogenetic resting spore (?) in rudimentary oogonium (?).
- Fig. 34. Antheridium (?) and oogonium (?) with oospore (?) connected by fusion canal (?).
- Fig. 35. Resting spore of *E. perforans*.

## PLATE 5



that the method of cleavage is fundamentally different in the Saprolegniaceae but primarily centrifugal in direction, because of the presence of a large central vacuole which displaces the protoplasm in a comparatively thin layer at the periphery. Doubtless when cleavage in *Eurychasma* and *Ectrogella* has been intensively studied from fixed and stained material the fundamental similarity of the process will become quite evident.

The secondary zoospores emerge from the cysts after a short dormant period (figs. 15, 20, 27). In *E. Gomphonematis* the numerous small granules present in the primary swarmers fuse during the encysted stage and form a single large refractive globule. These zoospores are oval and pyriform in shape with two unequal flagella inserted laterally or close to the anterior end. In motion the shorter flagellum is directed forward, while the longer one is dragged along behind (figs. 16, 21). Unlike those of the uniflagellate rhizidiaceous ehytrids the zoospores swim more evenly and do not dart about in a zigzag path.

Resting spores have so far been observed only in *E. perforans* (fig. 35) and *E. Liemophorae* (figs. 33, 34). In the former species no sexual fusion has been reported and the spores appear to be nothing more than spherical, thick-walled, encysted thalli or sporangia. In the latter species, however, Scherffel figured a thick-walled spore lying in a thin envelope with a hyaline thin-walled, empty vesicle or companion cell attached to one side by a broad tube (fig. 34). He regarded the resting spore as a oospore in a rudimentary oogonium which has been formed by fusion of the protoplasts of an antheridium and egg cell through a broad conjugation canal. Scherffel did not observe actual fusion in *E. Liemophorae*, and figure 34 may relate to nothing more than an irregular thallus, the content of which contracted into a thick-walled resting spore in the larger of the two lobes, as is suggested by figure 33. Resting spore formation of this type is not uncommon in species of the lower simple fungi, i.e., *Olpidium gregarium*, *Cantenaria Anguillulae*, etc. The evidence of sexual reproduction in *Ectrogella* is thus very meager and inconclusive, and until further proof is found the presence of sexuality in this genus must be regarded as highly questionable.

#### E. BACILLARIACEARUM Zopf, 1884, l.c., pl. 16, figs. 1-24.

*Cymbanche fockei* Pfitzer (pro parte), 1869. Sitzb. Niederrh. Ges. Nat. Heilk. 26:221.

*Olpidium gilli* de Wildeman, 1896. Ann. Soc. Belge Micro. 20:41; Gill, 1893. Jour. Roy. Micro. Soc., 1893:1, pl. 1.

Zoosporangia solitary or up to 30 in a cell, smooth, hyaline, oval, elongate, cylindrical, vermiform, 4-9  $\mu$  in diameter and up to 200  $\mu$  in length with 1 to 11 short exit tubes or papillae in single or opposite rows, which project between the separated valves of the diatom cell on the girdle side and stain intensely violet with chloro-iodide of zinc. Zoospores diplanetic; primary zoospores pyriform, 2  $\times$  4  $\mu$ ,

with a refractive spot at the anterior and numerous granules at the posterior end and two rudimentary (?) equally long, 4  $\mu$ , flagella inserted laterally in a slight indentation near the anterior end; emerging fully formed and swimming directly away, later coming to rest and encysting; secondary zoospores, oval 2  $\times$  4  $\mu$  (?) with a tapering anterior end, near which arise two unequal flagella, and one to several refractive granules near the posterior end. Resting spores unknown.

Parasitic in *Synedra lunularis*, *Synedra* sp.; *Gomphonema* sp. and *Pinnularia* sp. in Germany (Zopf, l.c.); *Synedra* sp. and *Gomphonema* sp. in Belgium (de Wildeman, '90, '93, '94, '95); *Pleurosigma attenuatum*, *Synedra* sp., *Pinnularia* sp., *Cocconema lanceolatum* and *Nitzschia sigmoidea* in England (Gill, '93; Smith and Ramsbottom, '17); *Synedra ulna*, *Pinnularia* sp., *Gomphonema* sp., and *Meridion circulare*, in Hungary (Scherffel, '25; Domjan, '35), and *Pinnularia* sp. in New York, U. S. A. (Sparrow, '33). This species was found in great abundance in *Nitzschia sigmoidea* by the author during the summer of 1942 at Beaufort, North Carolina.

This is the type species of the genus, and although it apparently occurs abundantly in nature it is still incompletely known. Petersen regarded it as a probable species of *Pleotrichelus* with numerous exit tubes arranged in rows.

The question of whether or not the organism which Gill described relates in entirety to this species has been the subject of much discussion. As is indicated in the synonymy above de Wildeman believed that the sporangia shown in figures 1-8 by Gill relate to a species of *Olpidium* since only a single elongate exit tube is present, while the thalli shown in figure 9 relate to *E. bacillariacearum*. Menden recognized *O. gilli* as a valid species, but Scherffel was undecided about its validity. He maintained, however, that it as well as Van Heurek's fungus is not identical to Zopf's or to any of his own species of *Ectrogella*, and believed that figure 9 of Gill may relate to *E. bacillariacearum* or *Aphanomycoptis*. Scherffel failed to observe Zopf's species in *Pinnularia* and *Gomphonema*, and he was accordingly of the opinion that Zopf's figure 23, plate 16, may relate to *Lagenidium brachystomum*.

Van Heurek ('99, p. 64, fig. 22) figured and described an endophytic parasite with a single elongate exit tube in *Pleurosigma angulatum* which is strikingly similar to Gill's organism. Van Heurek believed that his fungus may be identical to Gill's species.

As Fischer ('92) pointed out, Pfitzer's *Cymbanche fockei* may perhaps relate in part to *E. bacillariacearum*. Zopf ('84, '85), however, regarded it a member of the Saprolegniaceae. It is also possible that the thick-walled structure with an eccentric vacuole which Pfitzer described may be the resting spore of this species. Pfitzer described this spore as containing small starch grains like those found by Pringsheim in *Saprolegnia*, but these bodies are ob-

viously of a different nature than starch grains. The structures described for Föcke as spores of diatoms, which Pfitzer interpreted as a part of *Cymbanche föckei*, relate to a species of the Myxozoidia, *Gymnococcus föckei*, according to Zopf ('84b, pp. 120, 126) and Fischer.

**E. PERFORANS** Petersen. 1903. Over. Kgl. Dansk. Videns. Selsk. For. (5); 466, fig. VII, 1-8.

Zoosporangia solitary or up to 5 in a cell, smooth hyaline; wall staining light violet with chloro-iodide of zinc; spherical 20-35  $\mu$ , oval, elongate, 22-23  $\mu \times$  26-40  $\mu$ , sometimes slightly irregular, and becoming partially extramatrical at maturity with 1 to 8 short, very broad, 9-12  $\mu \times$  8-10  $\mu$ , exit tubes. Zoospores hyaline with a refractive globule at the anterior end, emerging fully formed and swimming directly away, pyriform and somewhat curved with the two flagella attached anteriorly (?) and oppositely directed in swimming, relative lengths of flagella unknown; motion during swimming uneven and twisting. Rest spores spherical, 14-19  $\mu$ , hyaline, smooth, thick-walled with one large or several smaller refractive globules; germination unknown.

Parasitic in *Licmophora Lyngbyei*, *Licmophora* sp., and *Synedra ulna* in Denmark (Petersen, l.c.; Sparrow, '34); *Licmophora abbreviata*, *Striatella unipunctata* and *Vorticella* sp., in Mass., U. S. A. (Sparrow, '36b), causing distortion of host cell and complete destruction of the host protoplasm. The author has recently ('42) observed this species in great abundance in *L. abbreviata* and *L. flagellata* at Beaufort, North Carolina.

This species appears to be a virulent parasite and may attain epidemic proportions in *Licmophora*, according to Sparrow ('36b). In the shape of its sporangia with numerous broad exit tubes this species is strikingly similar to *E. Licmophorae*, and Scherffel was accordingly of the opinion that the two species may prove to be identical. It is to be noted, however, that the base of the exit tubes of *E. perforans* is not thickened and does not form a spreading apparatus as in *E. Licmophorae*, nor do its zoospores encyst in a group at the mouth of the exit canals as far as is now known. It is primarily for these reasons that Sparrow ('34) regarded *E. perforans* as a distinct species. It is not improbable, however, that when intensive comparative studies have been made of both species and their range of variation worked out, they may prove to be identical.

Sparrow ('36) described the zoospores as possibly anteriorly biflagellate with both flagella oppositely directed in swimming. He was unable to determine the relative lengths of the flagella, and it is not known whether the zoospores are iso- or heterocont. Sparrow found that as much as eighty-eight per cent of the *Licmophora* cells in a single mount may be parasitized by this species. The zoospores are capable of attacking other hosts as well, since species of *Vorticella* which ingest free swimming zoospores may in turn be attacked by the swallowed parasites and completely destroyed.

No conclusive evidence of sexuality has been found in this species. Petersen found isolated thick-walled resting spores (fig. 35) in several instances, but these were not accompanied by empty antheridia or companion cells. Sparrow ('34), on the other hand, believed that the spores are surrounded by a thin envelope. In one instance he found an empty hemispherical cyst, 3  $\mu$  in diameter, attached to a fully mature spore. However, no stages of fusion were observed.

**E. MONOSTOMA** Scherffel, l.c., p. 8, pl. 1, figs. 10-19.

Zoosporangia solitary, elongate, tubular, somewhat spindle-shaped, 4-8  $\mu$  in diameter, slightly swollen in the median region from which a single, short, 2-3  $\mu$  thick, cylindrical exit tube or papilla arises; exit tube and part of the sporangium wall staining intensively violet with chloro-iodide of zinc. Primary zoospores aflagellate, gliding out of the sporangium and encysting in a group at the mouth of the exit tube; individual eystospores spherical, 6-8  $\mu$  in diameter, wall showing a marked cellulose reaction; secondary swimmers, lemon-shaped, 8  $\mu$  long, with a ventral furrow, heterocont (?), shorter flagellum directed forward and the longer one dragged along behind while in motion. Resting spores unknown.

Parasitic in *Synedra ulna* in Hungary; *Pinnularia* sp. in New York, U. S. A. (Sparrow, '33) and *Synedra* sp. in England (Sparrow, '36a).

According to Scherffel and Sparrow, this species differs from the other members of *Ectrogella* only by the presence of one short exit tube. Except for this character and the median bulge (fig. 19) its thallus and zoosporangia are identical to those of *E. bacillariacearum* which parasitizes the same host. Obviously the presence of one or more exit tubes is not always a distinctive specific character. However, the secondary zoospores of *E. monostoma* appear to be considerably larger (8  $\mu$  long) than those of *E. bacillariacearum* which Zopf reported to be only 2 to 3  $\mu$  in diameter. Zoospore size is a more constant specific cell character, and if further observations confirm this difference the validity of *E. monostoma* will be established.

**E. GOMPHONEMATIS** Scherffel, l.c., p. 9, pl. 1, figs. 20, 21.

Zoosporangia solitary, oval, oblong, egg-shaped with 1 or usually 2 short exit tubes located at the ends. Zoospores diplanetic, primary zoospores egg-shaped and somewhat elongate, 3  $\mu$  long, with a few highly refractive granules and the two equal flagella, slightly longer than the spore body, inserted almost at the apical end; swimming within the sporangia, later emerging singly and swimming away (?) or encysting in a group at the mouth of the exit tubes; granules fusing during encystment to form a large refractive globule as in some rhizidiaceous chytrids; germination of cysts, and structure of secondary zoospores unknown. Resting spores unknown.

Parasitic in *Gomphonema micropus* in Hungary.

Except for the oval shape of its thallus and zoosporangia (figs. 22–25) this species does not appear to have any particularly outstanding characters. Scherffel believed that the primary zoospores (fig. 26) may encyst at once at the mouth of the exit tube (fig. 27A) as in *E. bacillariacearum* and in *Achlya* species or swim away as in *Saprolegnia* and encyst later. Until more is known about this organism its validity as a distinct species will remain doubtful.

#### **E. LICMOPHORAE** Scherffel, l.c., p. 10, pl. 1, figs. 22–30.

Zoosporangia solitary or up to 10 in a cell, spreading open the diatom shell and becoming partially extramatrical at maturity; oval, slightly elongate with 1 to 10 exit tubes which are inflated, thick-walled, and flask-shaped at the base and give the mature sporangium and irregular, somewhat stellate appearance. Zoospore diplanetic; primary swarmers pyriform, 3  $\mu$  long, with two equal, apically inserted flagella which are approximately twice as long as the spore body; swarming within the sporangium, emerging singly and encysting in a group at the mouth of the exit tube; individual cysts 3.5  $\mu$  in diameter; germination of cysts and structure of secondary swarmers unknown. Resting spores single, hyaline and spherical, 12  $\mu$ , smooth and thick-walled; with several irregular refractive globules, lying in a spherical, 14  $\mu$  in diameter, cell or envelope which may be connected by a short broad canal or tube to an oval hyaline vesicle or companion cell; germination unknown.

Parasitic in *Licmophora* sp. in Hungary.

As has been noted before, Scherffel regarded the resting spore as a fertilized egg in a rudimentary oogonium, and in this respect he believed that *E. Licmophorae* may be closely related to *Aphanomyopsis* and *Olpidiopsis*. This species also shows considerable resemblance to *Eurychasma dicksonii* and *E. perforans* by its broad exit tubes and partially extramatrical zoosporangia. Whether or not it is distinct from the latter species remains, however, to be seen.

## EURYCHASMA

Magnus, 1905. Hedwigia 44: 347.

(PLATE 6)

Thallus intramatrical when young but becoming partially extramatrical at maturity; oval, ellipsoid, pyriform, dome-shaped, angular or irregular; transformed completely into a zoosporangium; wall of mature thallus well defined and showing a marked cellulose reaction when tested with chloro-iodide of zinc. Zoosporangia solitary in a cell, hyaline, smooth, oval ellipsoid, pyriform, angular or irregular with 1 to 3 broad exit papillae or short tubes which are usually completely extramatrical. Zoospores either

(1), coming to rest and encysting in the sporangium, forming thus a network of polygonal cysts as in *Dictyuchus*, later emerging from the cysts into the central portion of the sporangium and then swimming out; or (2), swimming out at once and pausing for a few moments at the mouth of the exit papilla, then gliding away without encysting. Zoospores ellipsoid and pyriform, hyaline, containing several small granules; heterocont with the two flagella attached near the anterior end. Resting spores unknown.

This genus includes at present two incompletely known species which are parasitic in brown and red algae. Our knowledge of the genus is based almost entirely on *E. dicksonii* the life cycle of which is illustrated in Plate 6. Until the last decade the zoospores were described as posteriorly uniflagellate, although in 1925 Scherffel predicted that further study would show them to be biflagellate. Dangeard's and Sparrow's studies in 1934 confirmed this prediction as is shown in figures 1 and 2. According to Sparrow, the zoospore comes to rest and encysts on the host cell (fig. 3) and soon forms a germ tube which penetrates the host cell wall. The content of the zoospore passes into the host as a naked body leaving the spore case and penetration tube on the outside (fig. 4) as in *Ectrogella*, *Pythiella*, *Olpidiopsis*, etc. Within the host cell the young parasite appears as a naked amoeboid protoplast (fig. 6) with one to several pseudopod-like extensions and resembles the early stages of *Ectrogella Licmophorae*. According to Lowenthal, it assumes a position near the host nucleus (fig. 6), but whether or not this migration takes place by independent amoeboid movement has not been determined. Lowenthal believed that it remains naked and surrounded by the host protoplasm until it is fairly large and multinucleate (fig. 7). In the early developmental stages it is hardly to be distinguished from the host protoplasm in living material, but as it increases in size it becomes very vacuolate (figs. 8, 9), according to Sparrow. Petersen ('05) described four distinct and successive maturation stages which he believed are also characteristic of the Chytridiales as a whole. At that time, however, it was generally believed that *Eurychasma* belonged among the chytrids. Since doubt has been expressed about the sequence of these stages it is worthwhile to enumerate them at this point: 1, *Stade protoplasmique ordinare* characterized by dense, almost avacuolate protoplasm and division of the nuclei; 2, *Stade globuleux* in which nuclear division and zoospore differentiation have been completed, and the sporangium is filled with numerous closely appressed globules of an oleaginous nature; 3, *Stade ecumeux* characterized by an increase in size of the sporangium, highly vacuolate protoplasm with the nuclei lying in the peripheral region and the cytoplasmic bridges separating the vacuoles, and by the disappearance of the outlines of the zoospores; and 4, *Stade a zoospores regulierement disposées contre la membrane* in which the zoospores are regularly distributed

around the inner periphery of the sporangium. In light of what has since been discovered about zoosporogenesis in *Pythiella*, *Ectrogella*, and other similar genera, it is very doubtful that numerous large vacuoles are present in the zoosporangium after the zoospores have been delimited, as Petersen reported for *stade ecumeux*. Before cleavage begins the vacuoles doubtless fuse to form one or more larger central ones (fig. 12) which apparently disappear when the centrifugal cleavage furrows reach the plasma membrane, as Scherffel and Couch have described for *Ectrogella* and *Pythiella*. It is, furthermore, questionable that nuclear division has been completed at the time of the *stade globuleux*. Petersen's studies relate only to living material, and in such preparations it is impossible to determine when nuclear division is finished. Petersen's report that these stages are characteristic of the Chytridiales as a whole was denied by Scherffel who maintained that they are typical only of the Saprolegniaceae and their close relatives. Both he and Lowenthal reported that the zoospores are delimited simultaneously, but this is probably incorrect. Cleavage is doubtless progressive as has been shown for other closely related genera.

According to Petersen, the zoospores become very active within the sporangium, and after a while come to rest and encyst around the inner periphery. They thus form by mutual contact and pressure a peripheral layer of polygonal cysts—the so-called "net-sporangium" stage (figs. 11, 14, 15). Sparrow, on the other hand, observed that the zoospores usually emerge at once and swim away (fig. 7) after a brief pause at the mouth of the exit tube. He found the "net-sporangium" stage only occasionally and concluded therefore that its occurrence may possibly be a reaction to adverse environmental conditions. Nevertheless, two types of zoospore behavior have been observed, one as in *Saprolegnia* and the other as in *Dictyuchus*. It differs from that of the latter genus, however, by the fact that the zoospores which emerge from the cysts do not pass through the sporangium wall but into the central cavity and then out through the exit tubes. Whether or not those which emerge directly and at once from the sporangium encyst after a period of motility as in *Saprolegnia* has not been determined. Petersen and Scherffel nonetheless regarded the zoospores of *Eurychasma* as diplanetic—the first motile stage occurring within the sporangium and the second on the outside. So far no one has figured or described the shape of the primary swimmers within the sporangium, nor the number, relative lengths, and position of their flagella.

The effect of *Eurychasma* on the host cell varies considerably as Rattray and subsequent workers have pointed out. In some instances the infected cells may not be greatly hypertrophied, while in other cases they may be several times their normal size. According to Sparrow, hypertrophy begins shortly after the entry of the parasite (figs. 3, 4, 5). However, infected cells are not stimulated by the

parasite to divide; nor do the adjacent healthy cells enlarge or divide as far as is now known. Hypertrophy is thus confined to infected cells. The enlargement of the host cell does not keep pace with the growth of the parasite, since the latter eventually bursts out of the confining host wall and is often one-third to one-half extramatrical at maturity as is shown in figures 10, 11, 14, 18, and 19. According to Lowenthal, destruction of the cell contents does not occur at once in *Pylaiella* cells, since the nucleus and plastids may be clearly discerned even when the parasite almost completely fills the cell. The pyrenoids, however, disappear very shortly. Sparrow, on the other hand, reported that the plastids of *Striaria* soon become discolored and disintegrate, and the degenerated protoplasm which is not utilized by the parasite eventually forms a brownish-green layer around the mature parasite.

Prior to the discovery that the zoospores of *Eurychasma* are biflagellate, this genus was generally included in the family Olpidiaceae of the Chytridiales, although as early as 1905 Petersen had made it the type genus of a new family, Eurychasmaceae, which he placed near the Olpidiaceae. Scherffel ('25), however, merged *Eurychasma* with *Ectrogella* and included it in the Saprolegniaceae, although it was not then known that the zoospores are biflagellate. He did this on the grounds that the thallus bursts out of the host cell as in species of *Ectrogella*; that the appearance of the protoplasm and the stages of zoosporogenesis are similar in both genera, and on the belief that the zoospores are typically diplanetic. It is to be noted, however, that the "net-sporangium" stage has not been found in species of *Ectrogella*. Furthermore, resting spores are unknown in *Eurychasma*, and since it is not improbable that they may be found to be quite different from those of *Ectrogella*, *Eurychasma* is retained here as a separate genus for the time being in the family Ectrogellaceae.

#### E. DICKSONII (Wright) Magnus, l.c., figs. 1-3.

*Rhizophidium dicksonii* Wright, 1879. Trans. Roy. Irish Acad. 26:369, Pl. 3.

*Olpodium dicksonii* (Wright) var. *Striariae* Wille, 1899. Vidensk. Selsk. Skr. Math. Nat. Klasse 1, 3:2, Pl. 3.

*Ectrogella dicksonii* (Wright) Scherffel, 1925. Arch. Protistk, 52:4, 11.

Zoosporangia solitary, hyaline, smooth, oval, ellipsoid, somewhat elongate,  $20-25 \mu \times 40-80 \mu$ , angular and slightly irregular with 1-3 short, broad, extramatrical exit tubes or papillae. Zoospores oval, pyriform  $3 \times 5 \mu$ , with two unequal flagella inserted near the anterior end. Resting spores unknown.

Parasitic in *Ectocarpus granulosus*, *E. crinitus*, *Pylaiella littoralis* and *Striaria attenuata* in Ireland (Wright, l.c.; Johnson, '09); *Ectocarpus confervoides*, *E. crinitus* and *E. pusillus* in Austria (Hauek, '78); *E. siliculosus* in Scotland (Rattray, '84); *Striaria attenuata* var. *fragilis* and *Pylaiella littoralis* in Norway (Wille, '99; Lowenthal, '05);

*P. littoralis*, *Stictyosiphon tortilis*, *Striaria attenuata*, *Akinetospora* sp., *Ectocarpus* sp., *E. conforvoides*, *E. sandrianus*, and *Punctaria* sp., in Denmark and Greenland (Petersen, '05; Sparrow, '34); *Stictyosiphon corbierei* and *Ectocarpus* sp. in France (Pierre Dangeard, '34), causing marked hypertrophy and destruction of the infected cells. Magnus ('05) claimed to have seen it in marine algae at Kiel also as early as 1872.

As is evident in the synonymy given above this type species of the genus has undergone numerous taxonomic changes. Wright, Hauck, Rattray, Fischer ('92) and Schroeter ('97) placed it in the genus *Rhizophidium*, but in '99 Wille transferred it to *Olpidium* because of the lack of a rhizoidal system. In 1905 Magnus called attention to the fact that the sporangia burst through the host cell and become partially extramatrical with one to several broad exit tubes or papillae, characters which are unlike those of *Olpidium*; and he accordingly created the new genus *Eurychasma* for Wright's species. Finally, in 1925, Scherffel transferred it to *Ectrogella*.

This species had doubtless been seen before its discovery by Wright and mistaken for a stage in the life cycle of its host. Wright and Rattray were of the opinion that the reproductive organs of certain marine algae described by Harvey (1862) and Küttzing (1855, 1861) relate to this species. Magnus, however, claimed that the latter workers had studied and figured *Chytridium plumulae*.

#### E. SACCOLUS Petersen, 1905, Overs. Kgl. Dansk. Videns. Selsk. Forh. (5):477, figs. VIII, 5, 8, 9.

Zoosporangia solitary, largely extramatrical, hyaline, smooth, irregular, elongate, 80–184  $\mu$  high, with one to three broad exit tubes; intramatrical portion lobed and irregular. Zoospores and resting spores unknown.

Parasitic in *Rhodymenia palmata* and *Halosaccion ramentaceum* in Greenland, causing marked hypertrophy and destruction of the infected cell.

According to Petersen, this species differs from *E. dicksonii* by the lobed and irregular shape of the zoosporangia, particularly the intramatrical portion. Although he did not observe the zoospores, he believed that they may behave in the same fashion as those of the previous species. On the basis of present-day knowledge concerning *Eurychasma* it appears to be a very doubtful species, and further study may prove it to be identical to *E. dicksonii*. Scherffel, on the other hand, believed that it may be a species of *Ectrogella*.

Whether or not Gran's ('00) *Olpidium Lauderiae* parasitic in *Lauderia borealis* belongs in *Eurychasma* or *Ectrogella* is a matter of dispute. Petersen (l.c., p. 469) regarded it as a questionable species of the former genus and renamed it *E. Lauderiae*. Scherffel thought that it may prove to be a member of *Ectrogella*, and named it *Ectrogella Lauderiae*.

## EURYCHASMIDIUM

Sparrow, 1936. Biol. Bull. 70: 241.

(PLATE 7)

Thalli intramatrical, solitary or numerous, unicellular, spherical, ellipsoid, irregular and lobed. Zoosporangia solitary or up to eight in a cell, variously-shaped with one or numerous exit tubes which may end flush with the surface of the host cell or extend beyond it. Zoospores diplanetic, encysting in polygonal cysts at the mouth of the exit tubes, emerging later and leaving the empty cysts behind; relative lengths and position of flagella unknown. Resting spores unknown.

Sparrow created this genus for the parasite of *Ceramium* which Magnus first discovered in 1872 and described as *Chytridium (Olpidium) tumifaciens*. As is shown in Plate 7 it is very similar to

#### PLATE 6

##### *Eurychasma dicksonii*

(Figs. 1, 3–5, 8–11, 14–17 after Sparrow, '34; fig. 2 after Dangeard, '34; figs. 6, 7, 12, 13 after Lowenthal, '05; fig. 18 after Wright, '77.)

Fig. 1. Fixed and stained biflagellate heterocont zoospores.

Fig. 2. Biflagellate heterocont zoospores with a tapering anterior end near which the flagella are attached.

Fig. 3. Early infection stage of *Striaria* cell.

Fig. 4. Enlarged algal cell with zoospore case and infection tube attached.

Fig. 5. Enlarged algal cell with small parasite within.

Fig. 6. Naked young uninucleate amoeba-like parasite with several pseudopods lying in cytoplasm of a *Pylaiella littoralis* cell; host nucleus at left.

Fig. 7. Naked tetranucleate parasite in which only two nuclei are visible; lying in the vacuole of a gametangium of *Pylaiella*.

Figs. 8–9. Distended host cells with vacuolate parasites; exit papillae beginning to form.

Fig. 10. Partially extruded parasite which has ruptured the enveloping host wall.

Fig. 11. Zoosporangium with a peripheral layer of zoospores.

Fig. 12. Longitudinal section of parasite before cleavage showing the protoplasm as a thin layer lining the sporangium.

Fig. 13. Longitudinal section of sporangium after completion of cleavage.

Fig. 14. A "net-sporangium" in which all but two of the zoospores have evacuated their cysts.

Fig. 15. Sporangium with two exit tubes and a peripheral layer of encysted zoospores.

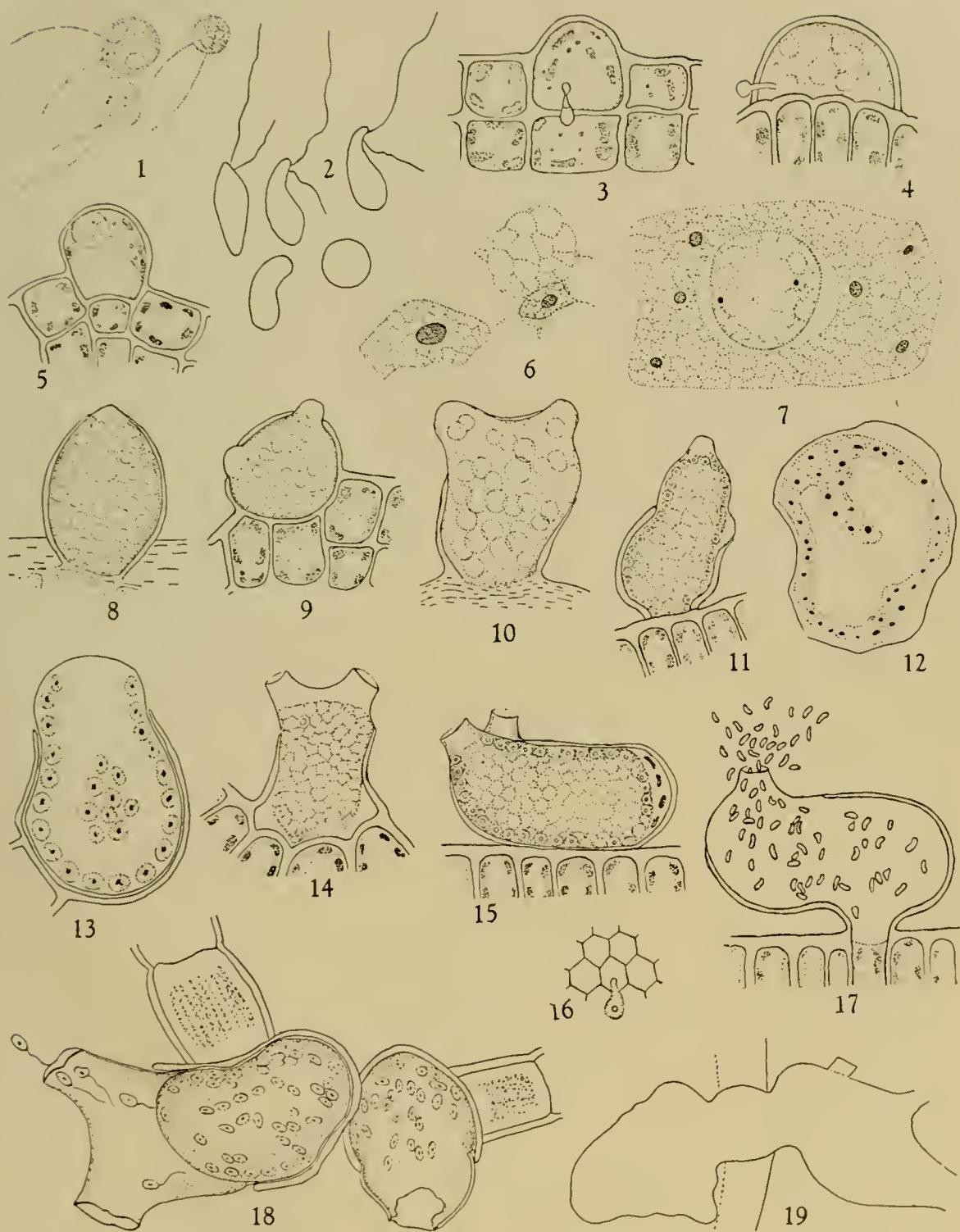
Fig. 16. Portion of a "net-sporangium" showing emergence of zoospore from a cyst.

Fig. 17. Sporangium showing direct discharge of zoospores without previous encystment.

Fig. 18. Sporangia in cells of *Ectocarpus granulosus*.

Fig. 19. Empty thallus of *Eurychasma sacculus* showing irregular sac-like character of intramatrical portion. Petersen, '05.

## PLATE 6



Eurychasma

*Eurychasma* in method of infection and development, but, according to Sparrow, it differs fundamentally by the presence of comparatively narrow exit tubes, its completely intramatrical position in the host, the encystment of the zoospores outside the sporangium, and by a more pronounced effect on the host cell. However, differences in number, length and diameter of the exit tubes, effect on the host, partial or complete intramatrical development are questionable generic characters, and when *Eurychasmidium* as well as *Eurychasma* are more fully known they may possibly prove to be identical.

Sparrow reported that zoospore germination and infection of the host are similar to those of *Eurychasma* and *Ectrogella*, although he did not actually observe these processes. In a few cases, however, he found empty zoospore cases and infection tubes attached to parasitized cells (fig. 6), which suggests that the contents of the spore enter the host cell as a naked body. Multiple infection apparently occurs fairly often, since as many as eight thalli may be found in a single cell (fig. 3). The well-established thalli are easily distinguishable in the host cell by the presence of numerous refractive globules in the protoplasm (figs. 5-9). As growth continues the chloroplasts begin to disintegrate and the remainder of the host protoplasm becomes quite vacuolate (figs. 6-7). Concomitant with these internal changes the host cell becomes distended and its wall greatly thickened (figs. 8-10). Infected cells do not divide, but healthy cells of adjacent nodes are stimulated to divide. There are thus formed in the vicinity of parasitized cells a number of curved stunted lateral branches (fig. 8, 9) which give a bushy appearance to the infected regions of the host plant.

The successive internal maturation changes in the parasite are identical to those described by Petersen for *Eurychasma*, including the characteristic "stade eumeux." The final stages in zoospore formation and emergence have not been observed, so that it is not known whether the zoospores become flagellate and swarm within the sporangium or glide out without flagella. In either event, they come to rest and encyst in loose masses at the mouth of the exit tubes (fig. 10). The cystospores thus formed (fig. 11) are polygonal in shape, and after a period of quiescence the protoplasm of each cyst emerges and develops into a flagellate zoospore. Sparrow reported that the zoospores are biflagellate, but he did not illustrate them and say whether they are iso- or heterocont, nor show at what place the flagella are attached. As far as the writer is aware the zoospores of this genus have never been illustrated.

#### E. TUMIFACIENS (Magnus) Sparrow, i.e., figs. 14-21.

Pl. 1, fig. 1.

*Chytridium (Olpidium) tumifaciens* Magnus, 1872a.  
Sitz'b. Gesell. Nat. Freunde Berlin, 1872:87. 1872b.

Jahresb. Komm. Untersuch. Deut. Meere Kiel 2:61.  
Pl. 1, figs. 1-16. 1873. Hedwigia, 12: 28.

*Olpidium tumifaciens* (Magnus) Fischer, 1892. Rabenhorst's Krypt. Fl. 1, IV: 27.

*Pleotrichelus tumifaciens* (Magnus) Petersen, 1905. l.c., p. 456.

Zoosporangia, hyaline and smooth, spherical, 100-110  $\mu$ , ellipsoid, 110  $\times$  200  $\mu$ , irregular and lobed with 1 to 30 exit tubes. Zoospores hyaline with a single refractive globule, elliptical, 3  $\times$  5  $\mu$ . Additional details are given in the generic diagnosis above.

Parasite in *Ceramium flabelligerum* and *E. acanthonotum* in Scotland (Magnus, i.e.) and England (Smith and Ramsbottom); a red alga in Belgium (de Wildeman '00); *Ceramium* sp. and *C. diaphanum* in the United States (Murray, '03; Sparrow, i.e.); and *Ceramium rubrum* in Denmark (Petersen, i.e.).

According to Magnus, this species was first observed by Cramer in 1855 (pl. 41, figs. 9, 11) at Naples, Italy, who mistook it for a monstrosity of *C. flabelligerum* (*C. spiniferum*). Sparrow believed that the organism which he observed at Wood's Hole is the same as Magnus' species, but there are some differences in the accounts of it given by the two authors. Magnus described the zoosporangia as solitary or numerous in a cell with one or two exit tubes which extend considerably beyond the algal cell, but he failed to observe any marked thickening of the host wall. Sparrow, on the other hand, reports that the wall is abnormally thickened, while the zoosporangia may possess as many as thirty exit tubes, through which the ellipsoid, biflagellate zoospores emerge. These differences may well be due to the limited observations of Magnus, but there is nonetheless a possibility that Sparrow may have studied a different species.

#### PLATE 7

##### *Eurychasmidium tumifaciens*

(Figs. 1-4 after Magnus, '72; figs. 6-11 after Sparrow, '36.)

Fig. 1. Young thallus in the apical hair cell of *C. flabelligerum*.

Fig. 2. Older thallus in same type of cell.

Fig. 3. Enlarged cell with eight spherical thalli.

Fig. 4. An enlarged apical cell containing a mature thallus with two broad exit tubes.

Fig. 5. Early developmental stage of thallus in *Ceramium diaphanum*.

Fig. 6. More mature thallus with zoospore case and infection tube still attached to the enlarging host cell.

Fig. 7. Thallus surrounded by vacuolate host protoplasm.

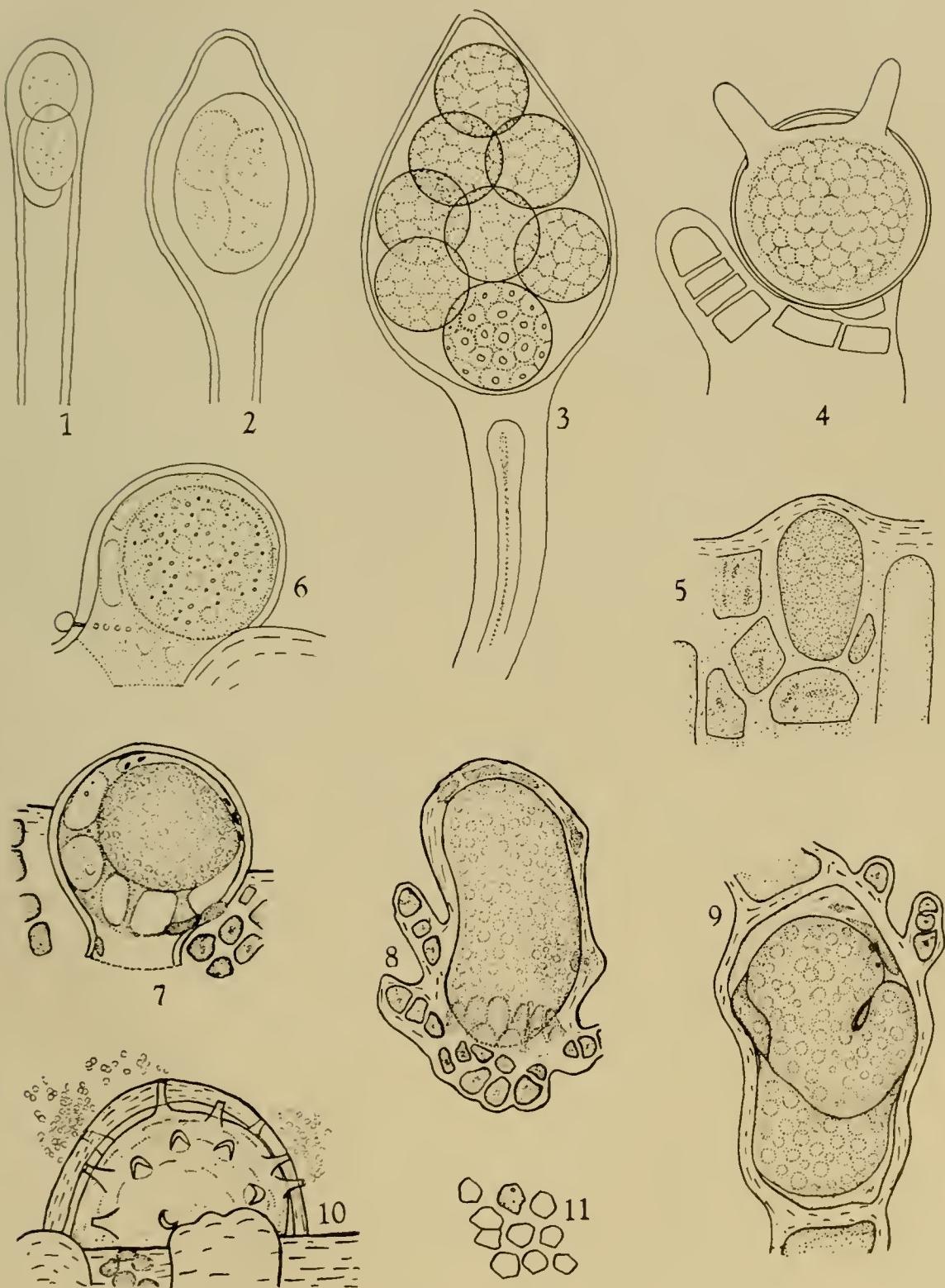
Fig. 8. Thallus completely filling host cell, the wall of which is greatly thickened.

Fig. 9. Lobed irregular, vacuolate thallus.

Fig. 10. Empty sporangium with numerous short exit tubes; groups of cystospores near the exit tubes.

Fig. 11. A group of polygonal cysts.

## PLATE 7



Eurychasmidium

## APHANOMYCOPSIS

Scherffel, 1925. Arch. Protistk. 52: 11.

(PLATE 8)

Thallus intramatrical, holocarpic, filamentous and thread-like or irregularly tubular, simple or branched, continuous or septate; walls showing a marked cellulose reaction when tested with chloro-iodide of zinc; whole thallus or segments transformed directly into sporangia or oogonia (?). Zoosporangia elongate, filamentous and cylindrical or short and tubular with one to several straight, curved or irregular exit tubes which project considerably beyond the surface of the host. Zoospores diplanetic, emerging in succession without flagella and encysting in a cluster at the mouth of the exit tube; secondary zoospores grape seed-shaped with a ventral furrow and conspicuous vacuole, isocont (?) or heterocont (?), active shorter flagellum directed forward in swimming with the longer one dragging behind; swimming movement relatively slow and even, not darting. Oogonia questionable. Resting spores or oospores (?) single or several in thallus or segments thereof; parthenogenetic (?), germination unknown.

Scherffel regarded this genus as closely related to *Ectrogella monostoma* and included it in the Saprolegniaceae near *Aphanomyces* because of its long thread-like zoosporangium and the formation of zoospores in single linear rows. He furthermore believed that the thalli of *Aphanomyopsis* with their incipient resting spores should be interpreted as rudimentary oogonia containing one or several egg cells which develop asexually or parthenogenetically, a viewpoint which was subsequently accepted by Sparrow ('33) and Coker and Matthews ('37). The latter workers, however, included *Aphanomyopsis* in the family Ectrogellaceae, and later on Sparrow ('42) followed this classification. Tokunaga ('33) on the other hand, placed it in the Lagenidiaceac. Scherffel pointed out that this genus differs from *Aphanomyces* by the lack of well differentiated zoosporangia and oogonia, but Tokunaga found the former structures to be strikingly like those of *Lagenidium*, as is shown in figures 15, 19, and 25. The segments which contain the resting spores are also similar in shape to the oogonia of some species of *Lagenidium*. The fact that the zoospores are diplanetic, encyst in clusters at the orifice of the exit tubes, and are heterocont after emerging from the cysts does not exclude this genus from the Lagenidiaceac since such characters are also to be found in *L. Oedogonii* and *Lagenidium* sp., Couch. Likewise, several species of the latter genus are parthenogenetic, but each so-called oogonium forms but one spore. On the bases of Tokunaga's studies, *Aphanomyopsis* is herewith included only temporarily in the Ectrogellaceac. It is not altogether improbable, however, that Tokunaga's fungus may be different from Scherffel's and Sparrow's species.

Further studies are therefore essential to a better understanding of the identity and relationships of *Aphanomyopsis*.

Scherffel reported that the zoospores which emerge from the cysts are heterocont (fig. 2), but Tokunaga described and figured them as isocont (fig. 16) without indicating any specific flagellum orientation during motility. After coming to rest on the host the zoospores form a broad germ tube which makes a small round hole in the silicified wall and penetrates the diatom cell (figs. 4, 5). The penetration tube continues to elongate, broadens, branches, and eventually develops into a full grown thallus, while the zoospore case and extramatrical portion of the tube remains attached on the outside (fig. 6). Scherffel and Sparrow reported only elongate, simple (fig. 13) or branched (fig. 17) non-septate thalli, but West and West and Tokunaga found that the thallus may be divided into segments by one to several septa (figs. 7, 15, 19, 25) at maturity.

One or more exit tubes are formed as the thallus develops, but they do not perforate the diatom cell like the penetration tube, according to Scherffel. Instead, they pass out between the valves of the host when young and then develop thickened walls at the region of exit, whereby the valves of the diatom are pushed apart (figs. 13, 18). This so-called "Spreizapparat" was observed by Scherffel and Sparrow, but Tokunaga did not illustrate it in his figures of

### PLATE 8

#### *Aphanomyopsis bacillariacearum*

(Figs. 1-6, 8-12, 14, 17, 18, 20-24 after Scherffel, '25; fig. 7 after West, '09; fig. 13 after Sparrow, '33; figs. 15, 16, 19, 25 after Tokunaga, '33.)

Fig. 1. Zoospore emerging from cyst.

Fig. 2. Laterally biflagellate heterocont zoospore.

Fig. 3. Optical cross section of same showing ventral groove and vacuole.

Figs. 4, 5. Infection of host.

Fig. 6. Empty zoospore case and infection tube on diatom cell.

Fig. 7. Branched septate thallus with zoospores clustered at tip of exit tube.

Figs. 8-11. Stages in cleavage and zoospore formation in exit canal.

Fig. 12. Branched exit tube with zoospores which failed to emerge from main branch.

Fig. 13. Two thalli with clusters of discharged zoospores, greatly enlarged.

Fig. 14. A thallus with three exit tubes.

Fig. 15. Branched septate thallus with several exit tubes.

Fig. 16. Bean-shaped isocont zoospores.

Figs. 17-19. Empty thalli. Note thickened basal portion of exit tube, the so-called "spreading apparatus."

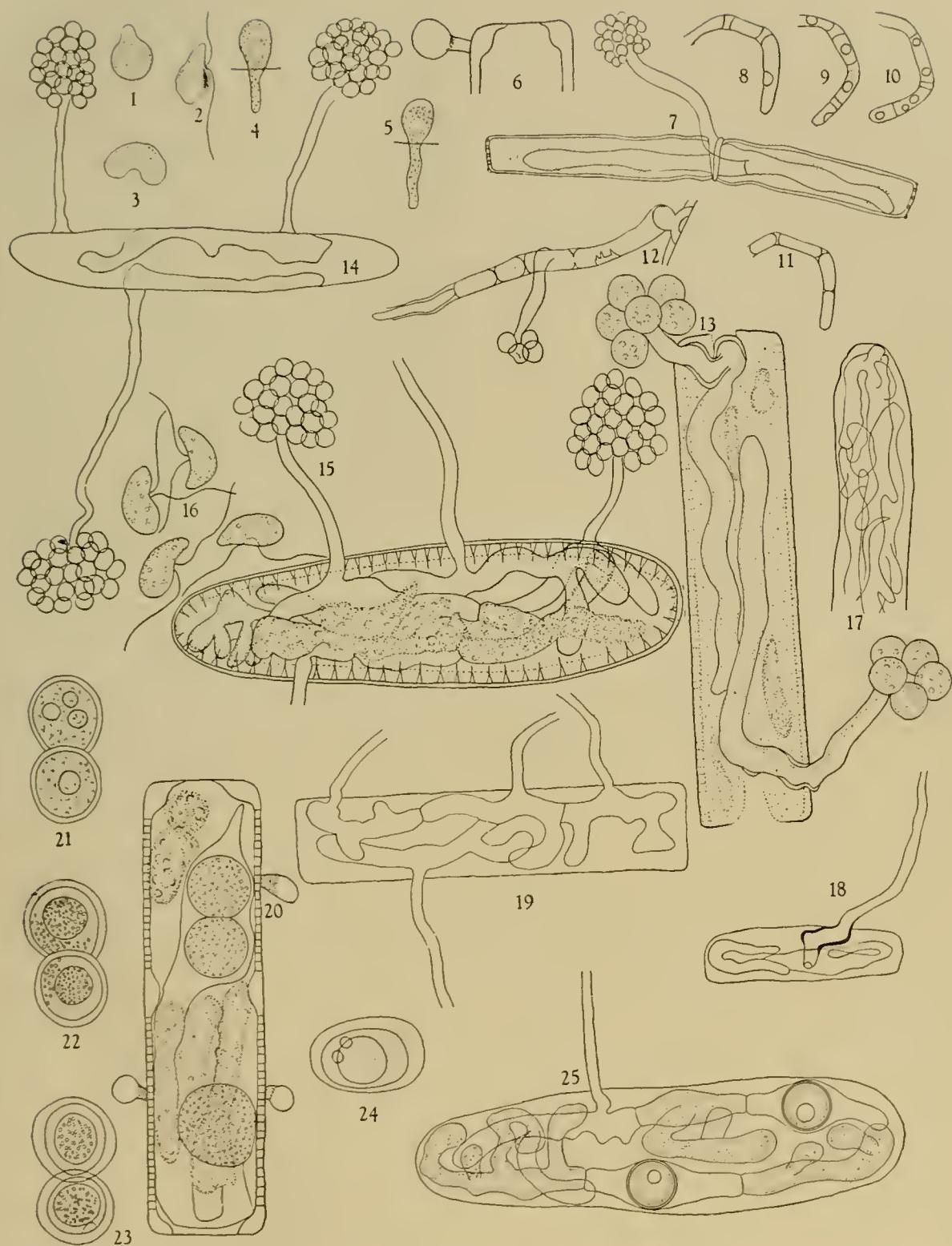
Fig. 20. Thallus with three young oospores (?), two of which occur in pairs.

Figs. 21-23. Developmental phases of the latter two oospores or resting spores.

Fig. 24. Large oval resting spore.

Fig. 25. Two branched septate thalli with oospores in two expanded cells.

## PLATE 8



Aphanomyopsis

this fungus. At maturity the protoplasm undergoes cleavage in the filamentous thallus and exit tubes, and forms elongate cylindrical segments (figs. 8-11) which then pass out in succession in a linear row as in *Aphanomyces*, according to Scherffel, round up, and form a cluster of cystospores at the mouth of the exit tube (figs. 7, 13, 14, 15). The lack of a differentiated sporangium in *Aphanomycopsis* is one of the chief characters which separates this genus from *Aphanomyces* in Scherffel's opinion, but it may be noted in this connection that Tokunaga found the sporangia to be delimited by cross walls from the remainder of the thallus.

So far no evidence of sexuality has been observed in *Aphanomycopsis*. Nevertheless, Scherffel regarded the thalli which bear one to several resting spores as rudimentary oogonia, but the evidence for this viewpoint is not convincing. In the process of resting spore formation the protoplasm of the entire thallus or segments thereof contracts into one or more globular portions (fig. 20) which develop thick, smooth hyaline walls and become dormant (figs. 21-24). Whether these spores give rise directly to zoospores or a germ tube in germination is not known.

**A. BACILLARIACEARUM** Scherffel, l.c., p. 14. Pl. 1, figs. 31-35; pl. 2, figs. 36-48.

Thallus 8-10  $\mu$  in diameter, continuous or septate, not markedly constricted at septa; branches often inflated at the end. Zoosporangia filamentous and thread-like, or cylindrical, tubular, unbranched or irregularly branched and lobed, 4.8-16.8  $\mu \times$  150  $\mu$ . Exit tubes 4.8-7  $\mu \times$  150-240  $\mu$ , thickened and inflated at base to form a so-called "spreading apparatus" for separating the valves of the diatom cell. Zoospore cysts at mouth of exit tubes spherical, 6-8  $\mu$ . Zoospores 7-8  $\mu \times$  10-12  $\mu$ . Entire thallus functioning as a rudimentary oogonium (?) in continuous specimen; oogonia (?) intermingled with sporangia in septate thalli, terminal or intercalary, cylindrical and medianly expanded, 15.6-26.6  $\mu$  in diameter, periplasm absent. Oospores (?) oval, 20  $\times$  24  $\mu$ , spherical 14.4-20  $\mu$ , hyaline, smooth and thick-walled with a large eccentric globule and a bright lateral spot. For further details see generic description above.

Parasitic in *Pinnularia viridis*, *Epithemia turgida*, *Cymbella gastrooides*, and *Nitzschia sigmaoidea* in Hungary (Scherffel, l.c.) *Pinnularia* sp., and *Syneandra* sp., in New York and England (Sparrow, '33, '36), *Surirella* sp., and *Navicula* sp., in Japan (Tokunaga, '34).

The parasite (fig. 7) which West and West described in *Pleurotaenium ehrenberghii* is very similar and probably identical to *A. bacillariacearum*. Their contention that this is the same fungus which Archer ('60) described from the same host seems very doubtful.

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## Chapter IV

## Olpidiopsidaceae

Sparrow, 1942, Mycologia 34: 113.

THIS FAMILY name appropriately replaces the Pseudolpidiaceae previously proposed by Petersen in 1909. Since *Olpidiopsis* was the first genus to be created for fungi of this type it is appropriate that the family take its name from this genus. Furthermore, there is considerable doubt about the validity of *Pseudolpidium* and should this genus prove to be synonymous with *Olpidiopsis* the name Pseudolpidiaceae would no longer be descriptive nor tenable. Petersen included two genera, *Olpidiopsis* and *Pseudolpidium*, in his family and placed it in the Lagenidiineae next to the family Lagenidiaceae. Sparrow likewise placed his Olpidiopsidaceae in the Lagenidiales but extended the family to include *Petersenia*, *Pythiella*, and *Pseudosphaerita* as well as *Olpidiopsis* and *Pseudolpidium*. Whether or not *Pseudosphaerita* belongs in this family is open to serious question, because nothing is known about the presence of sexuality and the nature of the resting spores in this genus. In the event it proves to be a valid genus of this family, Dangeard's Pseudosphaeritaceae may also be merged with the Olpidiopsidaceae. However, if Dangeard's ('33) and Mitchens ('28) reports that the thallus segments after each nuclear division are correct, *Pseudosphaerita* differs markedly from *Olpidiopsis* in method of development. The present writer is nevertheless including it here temporarily for want of a better group in which to place it. *Blastulidiopsis* is also included here provisionally for the same reason, although the development of the thallus by the enlargement, growth, and elongation of the intramatrical tip of the germ tube is more suggestive of relationship with the Lagenidiaceae than the Olpidiopsidaceae.

*Petersenia* is excluded from this family because the thalli of all known species, except *P. andreii*, are strikingly similar to those of *Sirolpidium* and *Pontisma* in the Sirolpidiaceae. According to Sparrow's account *P. andreii* is apparently a species of *Olpidiopsis* and is accordingly transferred to this genus. The inclusion of *Pythiella* in the Olpidiopsidaceae is likewise questionable. While its method of zoosporogenesis and behavior of the zoospores is similar to those of some *Olpidiopsis* species, the presence of periplasm in the so-called oogonium suggests a more direct relationship with the Pythiaceae. Furthermore, its walls give no positive cellulose reaction when tested with chloro-iodide of zinc, a character which is considered to be of fundamental significance in phylogeny and relationship. As it is herewith described, the Olpidiopsidaceae includes three incompletely known genera, *Pseudosphaerita*, *Blastulidiopsis* and *Pseudolpidium* in addition to

*Olpidiopsis* and *Pythiella*, genera which future studies may or may not prove to be closely related. As such it includes species with markedly heterocont and isocont zoospores, and is accordingly not a very coherent family of closely related genera. The sequence in which the genera are described below is no indication of their primitiveness or complexity.

## OLPIDIOPSIS

Cornu, 1872, Ann. Sci. Nat. 5 ser. 15: 114.

(PLATES 9 TO 13)

*Pleocystidium* Fisch. 1884, Sitz'b. Phys. Med. Soc. Erlangen 16: 60.

*Diphophysa* Schroeter, 1886, Cohn's Kryptog'fl. Schlesiens 3: 195.

*Olpidiopsis* (Cornu) Fischer, 1892, Rabenhorst's Kryptog'fl. I, 4: 37.

*Pseudolpidium* Fischer (pro parte) i.e., p. 33.

*Pseudolpidiopsis* Minden, 1911, Kryptog'fl. Mark Brandenburg 5: 255.

Thallus intramatrical, appearing more or less naked but immiscible with the host protoplasm when young but soon becoming invested with a cellulose wall. Zoosporangia solitary or numerous, up to 50 or more in a host cell, hyaline or greyish-granular, smooth or covered with non-cellulosic spines, knobs, or warts; spherical, oval, ellipsoid, fusiform, clongate, lobed, sac-like or irregular with one to several broad, tapering or cylindrical, straight, curved, coiled, short or elongate exit tubes which may end flush with the surface of the host cell or project beyond it. Zoospores hyaline with numerous minute refractive granules, and in some species containing a contractile vacuole; oval, ellipsoid, elongate, and slightly reniform, iso- or heterocont; flagella inserted laterally near the anterior end or anteriorly, shorter flagellum extending forward and the longer one backward in swimming; emerging fully formed and swimming directly away or occasionally lying quiescent in a mass for a few moments at the mouth of the exit tube before becoming actively motile; diplanetic in one species, primary swimmers aflagellate and amoeboid, or flagellate, encysting to form cystospores; movement of zoospores more or less even in swimming, not darting, interrupted by one to several rest periods during which the flagella may be retracted. Resting spores parthenogenetic or sexual; spherical, oval, ellipsoid or elongate, hyaline, golden, yellowish-brown or brown with a smooth or knobby, warty, spiny, undulating and

wavy exospore; warts, spines and knobs non-cellulosic; content coarsely granular with one to several large or small refringent globules; male or companion cells when present, single or numerous, oval, spherical, elongate or vermiform, hyaline, smooth or warty and spiny. Resting spores transformed directly into zoosporangia in germination and liberating zoospores through exit tubes.

### General Considerations

As is shown in the synonymy above species of this genus have undergone the usual taxonomic vicissitudes and have been bandied about from one genus to another. Cornu created the genus *Olpidiopsis* in 1872 for five parasites which he found in various species of the Saprolegniales. In three of these parasites he observed thick-walled resting spores to which were attached one or more smaller empty vesicles which he assumed to be male cells or antheridia. Although Cornu did not specifically mention the presence of attached cells as the distinguishing generic character of *Olpidiopsis*, it subsequently came to be regarded as such. Reinsch ('78) later observed the passage of the protoplasm of the small cell into the larger thallus, and since that time the resting spores of *Olpidiopsis* have been generally believed to arise from fusions of unlike and sexually differentiated thalli. In a subsequent study of these parasites, Fischer ('80) failed to find empty male companion cells attached to what he believed to be the resting spores of *O. Saprolegniae*. Accordingly, two years later ('82) he rejected the *cellule adjacente* character as diagnostic for the genus, and re-diagnosed and described *Olpidiopsis* as having asexual resting spores. Further studies in the meantime, however, convinced Fischer that his earlier observations were incorrect, and in 1892 he interpreted the genus in the original sense and established a second genus, *Pseudolpidium* for the *Olpidiopsis*-like species with asexual resting spores. In this genus he included *P. Saprolegniae* and *P. fusiforme*, for which he described resting spores, and four additional doubtful species in which resting spores were unknown.

In the meantime Zopf ('84) and Fisch ('84) had described two similar parasites, *O. schenckiana* and *Pleocystidium parasiticum*, with uniflagellate zoospores and sexual resting spores in *Spirogyra*. Two years later Schroeter established a new genus, *Diplophysa*, for Cornu's *O. Saprolegniae* and his own *D. elliptica* which parasitizes *Mesocarpus* sp. Fischer ('92), however, reduced *Diplophysa* and *Pleocystidium* to synonyms of *Olpidiopsis* and divided Cornu's genus into two subgenera—*Olpidiopsis* with biflagellate zoospores, and *Pleocystidium* with uniflagellate zoospores. In the former he placed *O. Saprolegniae* and *O. minor* (*O. fusiformis*), while *O. schenckiana* and *O. parasitica* were included in *Pleocystidium*. The sporangia and resting spores of several additional algal parasites were described by

de Wildeman in 1895, and in 1911 Minden established a new genus *Pseudolpidiopsis* (synonymous with *Pleocystidium* and *Diplophysa*), in the family Olpidiaceae for these species as well as *O. schenckiana* and *O. parasitica*. Inasmuch as the number of flagella on the zoospores of de Wildeman's fungi were unknown, Minden was not justified in referring these species to *Pseudolpidiopsis*. Since that time the zoospores of *O. schenckiana* and its synonym *O. parasitica* have been shown to be biflagellate and heterocont, so that *Pseudolpidiopsis* also becomes a synonym of *Olpidiopsis*. In the meantime, Butler ('07) added two additional species to the genus *Pseudolpidium*.

Since the time of Fischer and Butler until quite recently very little critical study was made of *Pseudolpidium*, although several new *Olpidiopsis* and *Pseudolpidium* species were described, and these two genera have been distinguished respectively by the presence and absence of male cells on the resting spores. In 1939, however, McLarty and Shanor independently discovered that the spiny structures which Fischer had interpreted as the resting spores of *Pseudolpidium* are nothing more than spiny evanescent zoosporangia, thus showing that Fischer's genus, based on the misinterpretation of these sporangia, is no longer valid. McLarty found in addition that the majority of resting spores of *O. Achlyae* develop parthenogenetically without sexual fusion, which suggests further that other *Pseudolpidium* species, i.e., *P. Pythii*, *P. gracile*, and *P. stellatum*, etc., with true resting spores lacking in attached male cells are only parthenogenetic members of *Olpidiopsis*. He ('41) accordingly amended the diagnosis of Cornu's genus to include such species and listed *Pseudolpidium* as a synonym. The present writer is following this diagnosis almost completely but retaining *Pseudolpidium* provisionally as a dumping ground for the species in which no resting spores have yet been found, i.e., *P. Glenodinianum*, *P. Sphaeritae* and *P. deformans*. The first two of these species will probably be included eventually in *Olpidiopsis*, but *P. deformans*, because of its amoeboid schizogonic thallus, appears to belong to a different group of organisms.

McLarty and Shanor furthermore demonstrated quite clearly from monozoospore infection experiments that the number, size and shape of the zoosporangia as well as the character of the spines, warts, and knobs on the resting spores are highly variable and of little diagnostic value in distinguishing closely-similar species. It is accordingly almost impossible to determine with certainty the identity of most of the *Saprolegnia*- and *Achlyea*-inhabiting species which were only briefly and meagerly described prior to 1939 and 1941. Until all species have been as intensively studied as *O. varians* and *O. Achlyae*, an accurate diagnosis of this genus is well-nigh impossible, and for this reason the classification given below is to be regarded as temporary.

Particularly significant in diagnosis are the results of Shanor's ('40) and Miss Whiffen's ('42)

Table 1, showing the host range of five species of *Olpidiopsis*. Numerals indicate number of monospore infections attempted; + and — below numerals, success or failure to secure infection; and H, the original host from which each parasite was isolated. From Shanor, 1940.

Parasites	Hosts																								
	<i>Achlya racemosae</i>	<i>A. colorata</i>	<i>A. americana</i>	<i>A. proliferidae</i>	<i>A. flagellata</i>	<i>A. imperfecta</i>	<i>A. Klebsiana</i>	<i>A. recurva</i>	<i>A. apiculata</i>	<i>A. glomerata</i>	<i>Aphanomyces laevis</i>	<i>Aphanomyces Trelaeanus</i>	<i>A. stellatus</i>	<i>Dicyclonus sp.</i>	<i>Isoachlya muscicola</i>	<i>I. unispora</i>	<i>I. eccentrica</i>	<i>Leptolegnia</i> sp.	<i>Protachlya paradoxa</i>	<i>Saprolegnia declina</i>	<i>S. delica</i>	<i>S. ferax</i>	<i>S. mixta</i>	<i>S. monoica</i>	<i>S. littoralis</i>
<i>Olpidiopsis varians</i>	4 +	4 +	3 —	2 —	11 +	8 —	2 —	2 —	2 —	2 —	2 —	2 —	2 —	2 —	2 —	2 —	2 —	2 —	2 —	2 —	2 —	2 —	2 —	2 —	
<i>O. fusiformis</i>	4 +	4 —	3 —	2 —	7 +	11 +	2 —	2 —	2 —	2 —	2 —	2 —	2 —	2 —	2 —	2 —	2 —	2 —	2 —	2 —	2 —	2 —	2 —	2 —	
<i>O. Saprolegniae</i>	2 —	2 —	2 —	2 —	2 —	2 —	2 —	2 —	2 —	2 —	2 —	2 —	2 —	2 —	2 —	1 +	4 +	4 +	2 +	2 +	H +	1 +	1 +	1 +	2 +
<i>O. incrassata</i>	2 —	2 —	2 —	2 —	2 —	2 —	2 —	2 —	2 —	2 —	2 —	2 —	2 —	2 —	2 —	3 +	4 +	2 +	2 +	1 +	1 +	H +	1 +	2 +	
<i>O. luxurians</i> ( <i>O. Aphanomyces</i> )	2 —	2 —	2 —	2 —	2 —	2 —	2 —	2 —	2 —	2 —	2 —	2 —	2 —	2 —	2 —	2 —	2 —	2 —	2 —	2 —	2 —	2 —	2 —	2 —	

cross inoculation experiments involving numerous host species of *Saprolegnia*, *Achlya*, other related genera, and *Pythium*. As is shown in table 1, Shanor found that *O. fusiformis* and *O. varians* are restricted in host range to a few species of *Achlya*, while *O. Aphanomyces* (*O. luxurians*) is limited to *Aphanomyces laevis*. Miss Whiffen, however, found a form of the latter species on *A. cladogamous* which would not infect *A. laevis*. *Olpidiopsis Saprolegniae* and *O. incrassata*, on the other hand, are restricted to the same species of *Saprolegnia* and to all but one, *I. eccentrica*, of the same species of *Isoachlya*, according to Shanor. The number of infections attempted by Shanor, however, is small, and more extensive tests may possibly give different results. Furthermore, it is not evident from Shanor's account that temperature, pH concentration, and other environmental conditions were controlled in his experiments. Such factors have proven to be very significant in infection and development of other fungus diseases, and it is quite probable that they operate in relation to *Olpidiopsis* also. Nonetheless, the obligate parasitism and limited host range of *Olpidiopsis* species which parasitize the *Saprolegniaceae* have been clearly established. Shanor's results are furthermore significant, because they suggest that species which were formerly believed to be distinct, *O. Aphanomyces* and *O. luxurians* for example, may be identical. This is further substantiated by the observations that these species are not as distinct morphologically as they were earlier reported to be.

The data presented by McLarty and Shanor show very definitely that hasty observations and meager descriptions, of the kind so frequently made in the past, without exact identification of the host and in-

tensive study of the range of morphological variation, are practically worthless in the study of *Olpidiopsis*. Further studies on these parasites of *saprolegniaceous* hosts, if they are to be of value, must comply with the following criteria: 1, Exact identification of the host from pure cultures; 2, Monospore infections of a pure culture of the host to determine whether one or more parasite species are present in the original host culture; 3, Intensive study of monospore infection cultures of the parasite to determine the variations in size, shape, and echinulation or spininess of the sporangia, in the degree of sexuality present, and in the character of the outer resting spore wall; 4, Extensive inoculation of *saprolegniaceous* hosts to determine the host range.

### Development of Thalli and Zoosporangia

The development and life cycle of *Olpidiopsis* species are as follows: The zoospore comes to rest on the host cell, develops a definite cellulose wall (fig. 8) and forms a conspicuous germ tube through which the content of the spore passes into the host (figs. 9-11), leaving the empty case on the outside. Occasionally, the germ tube fails to penetrate the host and may elongate and branch to a marked degree. Figure 7 shows a spore which germinated in water outside of the host and formed a branched germ tube which is strikingly similar to the rhizoidal system of a young rhizidial chytrid thallus. The newly-entered zoospores and young thalli are apparently naked but immiscible with the host protoplasm. Even after ten hours following entry into the host McLarty was unable to demonstrate the

presence of a structural cellulose wall by plasmolytic experiments and treatment with chloro-iodide of zinc. According to Scherffel and Diehl, the young parasite may change its shape and position and independently undergo slight amoeboid movement, but McLarty maintained that in *O. Achlyae*, at least, such changes are caused by the rapid streaming of the host protoplasm in which the parasite is passively carried along (figs. 12-15). In *O. andréi* (*P. Ectocarpi*) Jokl figured the young thallus as an amoeba with one to several long, more or less radially oriented pseudopods (fig. 162) which migrates towards and engulfs the host nucleus. Fischer and Scherffel also have shown that the young thalli of *O. schenkiana* (*P. parasiticum*), and *O. Oedogoniorum* respectively are often to be found in close association with the host nucleus (fig. 133) which suggests that the food supply may be more optimum in that region of the host cell.

All present-day workers are agreed that no fusion of young thalli or newly-entered zoospores to form a plasmodium occurs in *Olpidiopsis*. The monospore infection experiments of McLarty and Shanor show conclusively that each zoospore gives rise to a single independent thallus or sporangium. By the time the thallus has attained mature size it is invested by a definite wall which in most species has been shown to give a marked positive cellulose reaction when tested with chloro-iodide of zinc. This wall is evidently formed by the parasite itself, but the knobs, warts, and spines which may later appear on it apparently have a different origin. As Fischer has shown, globules and masses of transformed host protoplasm accumulate at separate points around the periphery of the thallus wall (fig. 31) and are gradually transformed further into spines, warts, and other excrescences (fig. 32). These spines show no positive cellulose reaction when tested, which further suggests that they are different from the primary wall. Inasmuch as they are formed in this manner, it is to be expected that they will vary markedly in size, length, and shape. As is shown in figures 26 to 30 they may be lacking entirely or cover only a part of the sporangium (fig. 26) and vary from blunt knobs to broad or fine spines. Spininess of the sporangia can therefore no longer be regarded as a specific character.

The protoplasmic changes which occur during the growth, development, maturation and cleavage of the thalli and zoosporangia have been intensively studied in living as well as fixed material of several *Olpidiopsis* species, particularly *O. Saprolegnia*, *O. Aphanomyces*, and *O. Achlyae*. Successive stages of these changes are illustrated in figures 16 to 25 of two sporangia of *O. Achlyae*. The young developing thallus usually includes numerous fatty refractive bodies, and as it grows in size, the latter increase in number and size and impart a granular and slightly yellowish gleam or refringent appearance to the protoplasm (fig. 16). With further development these globules gradually become broken up into bodies of smaller size and appear as oily droplets

suspended in the more homogeneous protoplasm (fig. 17). At this stage of development small vacuoles appear in the protoplasm (fig. 17), and as they become more distinct they begin to coalesce. The protoplasm at this stage appears granular and slightly brown in appearance, and when stained with Sudan III it becomes brick-brown in color. Coalescence of the vacuoles continues until one or more large central ones are formed (fig. 19). Within an hour following this stage the vacuoles begin to undergo changes in shape (fig. 20) which may continue for a few minutes to half an hour. Cleavage furrows then begin to form at the periphery of the vacuoles and travel centrifugally to the plasma membrane (fig. 21) and delimit the initial zoospore segments (fig. 22). However, in *O. Achlyae* the areas previously occupied by the vacuoles as such do not disappear as the cleavage furrows cut through the plasma membrane as Schwartze ('22) described for *O. Saprolegniae*. In-

#### PLATE 9

##### *Olpidiopsis Achlyae*

(All figures after McLarty, '41)

Fig. 1. Slightly bean-shaped living zoospore with vacuoles and refractive granules.

Fig. 2. Fixed and stained zoospore with large nucleus. Slightly unequal flagella inserted beside a deep-staining body near the anterior end.

Fig. 3. Amoeboid zoospore.

Fig. 4. Zoospore retracting flagella before going into a temporary rest period.

Figs. 5, 6. Zoospore at rest.

Fig. 7. Zoospore germinated in water with a branched, rhizoid-like germ tube.

Fig. 8. Zoospore at rest and encysted on surface of host hypha.

Figs. 9-11. Successive infection stages.

Figs. 12-15. Changes in shape of the newly-entered parasite due to the streaming of the host protoplasm.

Fig. 16. Two incipient zoosporangia surrounded by a dense layer and radiating strands of the host protoplasm.

Figs. 17-20. Successive maturing stages of two zoosporangia.

Figs. 21-25. Cleavage and sporogenesis of lower sporangium shown in previous figures.

Fig. 26. Smooth and partly-spiny zoosporangia.

##### *O. varians*

Figs. 27-30. Variations in the character of the sporangium wall. Shanor, '39.

##### *O. fusiformis*

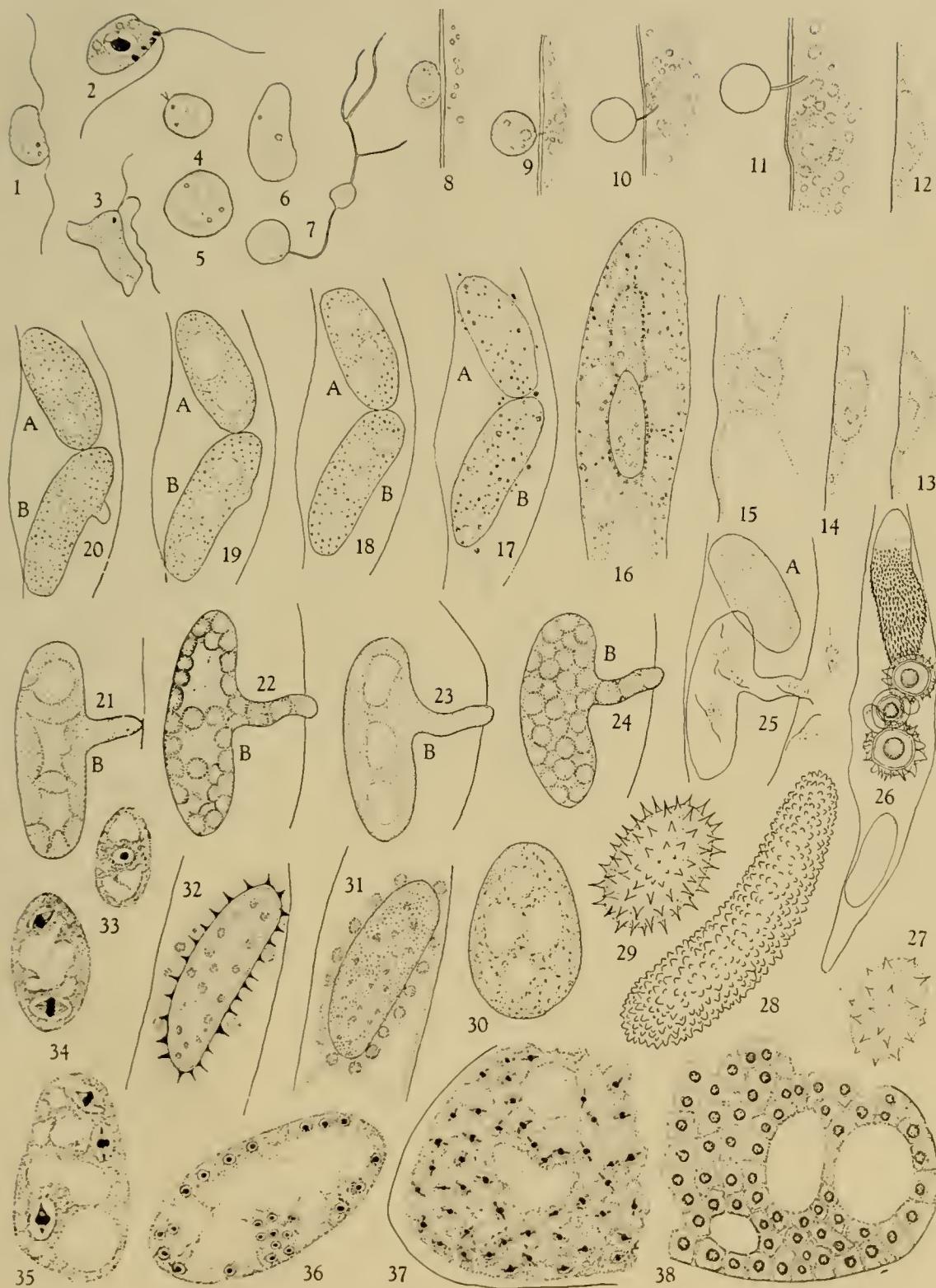
Figs. 31, 32. Formation of spines on zoosporangia. Fischer, '82.

##### *O. texans*

Figs. 33-37. Successive stages in the development of a thallus from fixed and stained material. Nuclear division simultaneous and completely synchronous. Barrett, '12.

Fig. 38. Portion of a zoosporangium following cleavage. Vacuolar areas still present. Barrett, l.c.

## PLATE 9



stead, McLarty found that for about a minute following the completion of cleavage the zoospores remained faintly visible flanking the irregular vacuolar spaces (fig. 22). Then as the protoplasm becomes more homogeneously granular and somewhat oleaginous in appearance again, the outlines of the zoospores disappear, and the vacuoles regain their even contours (fig. 23). This is the so-called homogeneous stage following cleavage which has been described by most students of *Olpidiopsis*. Sporangia in the stage illustrated in figure 23 may undergo a prolonged rest period before liberating the zoospores. That the zoospore initials do not become confluent during the homogeneous stage, as Butler ('07) believed, is shown by McLarty's plasmolytic experiments on sporangia in this stage. After a period of about three quarters of an hour the zoospore segments become visible again (fig. 24), and shortly thereafter the vacuolate areas disappear suddenly and entirely. The zoospores soon assume their mature shape and begin to swarm in the sporangium, and within a few minutes following this stage, the tip of the exit tube opens. The zoospores then emerge fully developed and swim directly away (fig. 25).

Variations of the type of cleavage and zoospore behavior described above for *O. Achlyae* have often been reported. In *O. Saprolegniae* and *O. Oedogoniiorum*, for example, Coker ('23) and Scherffel ('25) noted that the whole content of the zoosporangium may occasionally emerge to the outside as a globular, naked, undifferentiated, protoplasmic mass and then undergo cleavage into zoospores as in *Lagenidium* and *Pythium*. In *O. Pythii* the zoospores swarm for a brief period at the mouth of the exit tube (fig. 114) and then come to rest in a cluster, according to Butler. After a few minutes motion is resumed, and the zoospores, which are by this time provided with two flagella, swim away. A similar behavior for the zoospores of *O. schenkiana* was reported by Scherffel (figs. 137, 138). This initial rest period at the mouth of the exit tube and the subsequent ones which interrupt the active swimming stage have been interpreted by Butler, Barrett, Scherffel, and Diehl as evidence of primitive or rudimentary diplanetism. In coming to rest the zoospores may retract their flagella (fig. 4) and assume spherical or elongate shapes (figs. 5, 6) but they do not encyst. At least no empty vesicle is left behind as they form new flagella and swim away. In *O. Oedogoniiorum*, on the other hand, Scherffel reported true diplanetism. The primary swimmers are laterally biflagellate (fig. 153). The cystospores later germinate, and an empty vesicle is left behind as the secondary swimmer emerges. Whether or not the position of the flagella on the secondary swimmers differs from that of the primary swimmers is not known.

The accounts and descriptions in the literature on the shape of the zoospores and relative lengths of the flagella vary considerably. Most investigators have described the zoospores as oval, elongate, and tapering at the anterior end or somewhat reniform with-

out a marked ventral furrow and with two flagella of equal or almost equal length inserted in or near the anterior end. Other workers have reported them to be almost spherical, oval, pyriform and distinctly heterocont (figs. 103, 158). Accurate data on the exact location and relative lengths of the flagella are lacking in most species. However, since the zoospores swim fairly rapidly and undergo changes in shape it is difficult to determine with certainty the relative lengths of the flagella in living material. Markedly heterocont zoospores have been reported and figured for *O. irregularis* (Constantineanu, '01), *O. schenkiana* (Scherffel, '25), and *O. Ricciae* (du Plessis, '33), while in the remaining species they have been described as isocont or with flagella of

#### PLATE 10

##### *O. Achlyae*

Figs. 39-53. Successive stages of nuclear division. McLarty, l.c.

##### *O. luxurians*

Fig. 54. Two young incipient zoosporangia and a larger female thallus with an attached male thallus in a swollen hyphal tip. Barrett, l.c.

##### *O. Achlyae*

(All drawings after McLarty, l.c.)

Figs. 55-58. Successive stages in the development of a parthenogenetic and a sexual spore. Incipient spores in figure 55 surrounded by a hyaline, amorphous zone or layer.

Fig. 59. Incipient spore from fixed and stained material showing centripetal development of spines at localized points.

Fig. 60. Remnant of border of amorphous zone forming a membrane-like border around the tips of the spines.

Figs. 61-67. Variations in the character of the exospore.

##### *O. vexans* and other species

Fig. 68. Young male and female thalli; nuclei dividing. Barrett, l.c.

Figs. 69-76. Stages in nuclear division from female thallus. Barrett, l.c.

Fig. 77. Gelatinization of intervening wall between the male and female thalli prior to plasmogamy. Barrett, l.c.

Fig. 78. Later state in gelatinization. Nuclei in small male thallus dividing. Barrett, l.c.

Fig. 79. Passage of male nuclei into female thallus. *O. luxurians*. Barrett, l.c.

Figs. 80-82. Nuclear pairing and karyogamy. *O. vexans*. Barrett, l.c.

Fig. 83. Mature resting spore with two attached male thalli which still contain their protoplasm. *O. Achlyae*. McLarty, l.c.

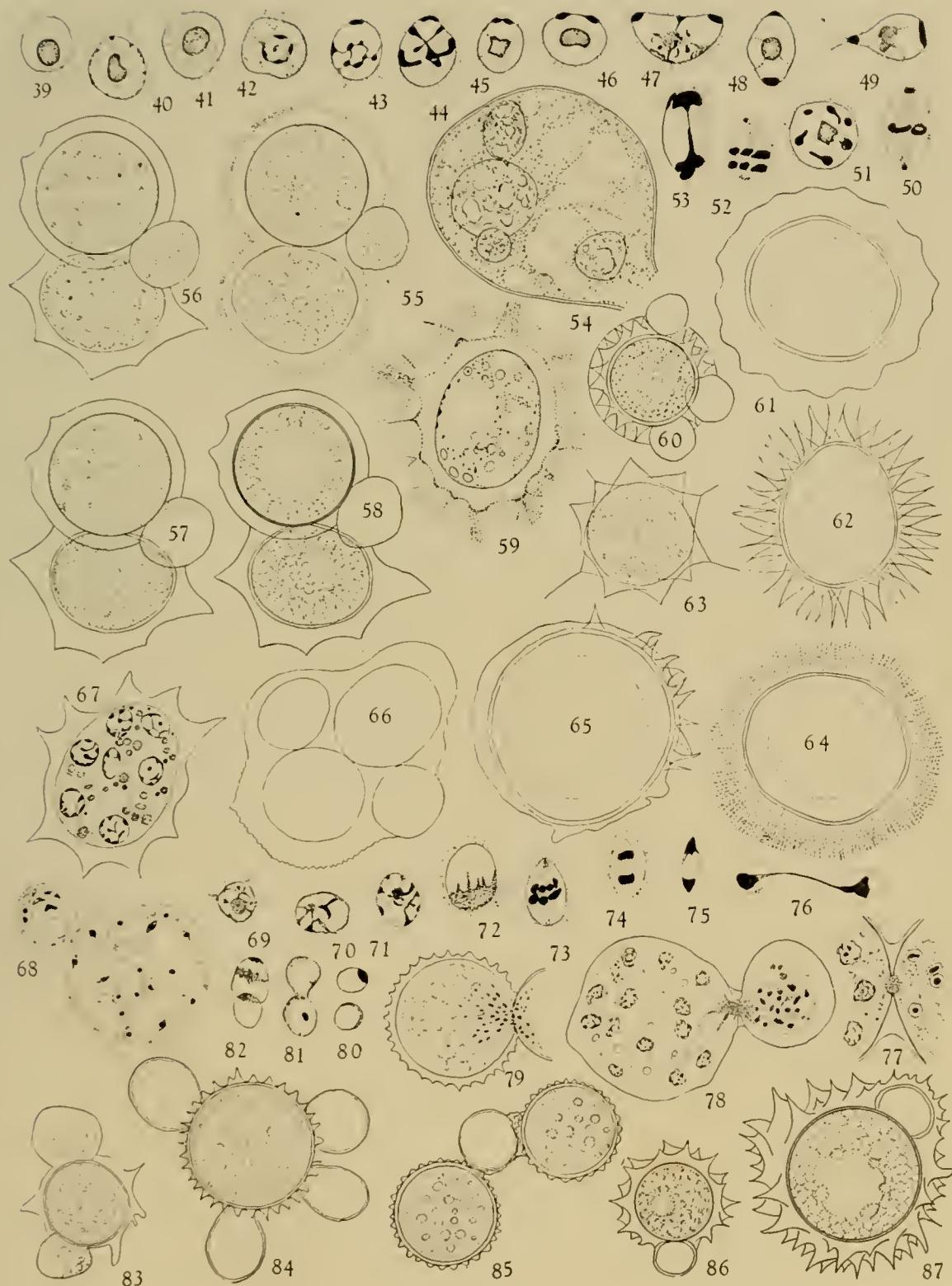
Fig. 84. Resting spore with four attached empty male cells.

Fig. 85. One empty male thallus between two resting spores. *O. luxurians*. Barrett, l.c. Drawn from photograph.

Fig. 86. Small *O. minor*-like resting spore of *O. varians*. Shanor, '39a.

Fig. 87. Early germination stage. Male thallus enveloped by spiny exposure. *O. varians*. Shanor, l.c.

## PLATE 10



"about" equal length. Whether or not the heteroecous species should be segregated in a separate group on this basis is of questionable diagnostic value until the zoospores of all species have been intensively studied. According to Couch ('41) one of the flagella of *O. Saprolegniae* has a long distinct tail piece, while the other one possesses nine to eighteen lateral "tinsel" cilia, 1.5  $\mu$  long, which may occur on one or both sides or follow a spiral course. The same type of flagella will probably be found to occur in all species of *Olpidiopsis*.

During growth and development of the thalli the nuclei undergo simultaneous and synchronous division (figs. 34, 35, 37), according to Barrett and McLarty. Nuclear division is typically indirect and not of the so-called promitotic type reported for the Plasmodiophorales, although the resting nuclei possess a very large nucleole and little chromatin in the form of granules on a reticulum (fig. 39). Successive division stages from thalli of *O. Achlyae* are shown in figures 39 to 53. The fact that most of the stainable material is in the form of a globular nucleole which often appears to be vacuolate or made up of differentially stainable regions (figs. 41, 42) suggested to McLarty that the nucleole functions as a storehouse of chromatin. This is further substantiated, in his opinion, by the radial orientation of the chromatin network on the nucleole (figs. 40, 41) and the latter's gradual disappearance as the prophase changes progress. Barrett, on the other hand, found a well-defined dense chromatin reticulum in addition to a large nucleole in resting nuclei of the female thalli (figs. 58 to 60). McLarty interpreted the emergence of radially oriented chromatin threads as the beginning of the prophases (figs. 40, 41), and as these stages progress the chromatin becomes more evident as globular (fig. 43) or rod-shaped densely stained bodies (fig. 44). By this time the nucleole has usually disappeared. Concurrent with the emergence of chromosomes a deeply stainable centrosome-like body appears at one of the nuclear poles in *O. Achlyae* (fig. 43) and undergoes division (figs. 45, 46). The daughter bodies thus formed then gradually migrate around the nuclear membrane (fig. 47) to the opposite poles of the nucleus (figs. 48, 49, 50). Barrett, however, found no evidence of centrosomes in *O. vexans*. No conspicuous astral rays have been found in association with these bodies in *O. Achlyae*, nor does the division spindle appear to arise from them as far as is now known. According to Barrett, the latter originates from the chromatin mass in the equator of the nucleus and gradually grows towards the poles, but his figures of the process are not definite and clear. In profile views of the equatorial plate stages the chromosomes are often arranged in a broken ring (fig. 50) around the margin of the spindle, but usually they are closely crowded together and appear as a dark band. In polar views of this stage (fig. 51) McLarty found six chromosomes in *O. Achlyae* which is the same number reported by Barrett for *O. vexans*. No evidence of meiosis has been found in these divisions in

the thalli and zoosporangia. The halves of the chromosomes separate in the metaphases and migrate (fig. 52) to the poles as two compact deeply stained masses (fig. 53), which may often be connected by a slender chromatin filament (figs. 53, 76). The nucleus and spindle elongate considerably in the late prophases and metaphases, and by the time of the late anaphases the nuclear membrane has usually disappeared entirely. The formation of the daughter nuclear membranes and the telophasic reconstruction stages of the nuclei are not well known, although figure 76 suggests that the daughter chromosome groups become surrounded by clear spaces, the boundaries of which later become the nuclear membranes. Nuclear division in the so-called antheridia and oogonia is also mitotic (figs. 68 to 76). In *O. vexans*, however, Barrett found prophase stages in which the chromatin was aggregated in synaptic-like masses at one side of the nucleus (fig. 72), but he did not believe that they relate to prophasess of meiosis.

### Resting Spore Development and Sex Differentiation

As has been noted in the generic diagnosis above the resting spores of *Olpidiopsis* may develop parthenogenetically without sexual fusion or as the result of fusion of a large female thallus with one to several smaller male thalli. Some species, i.e., *O. gracile* and *O. Pythii*, appear at present to be wholly parthenogenetic, while others are only partially so or entirely sexual. The small male and larger female thalli are generally referred to in the literature as antheridia and oogonia, respectively, and the fusion of these cells has been regarded as a primitive or rudimentary type of heterogamous and oomyctous sexual reproduction. Petersen and Seherffel regarded the resting spores of *Olpidiopsis* as an oospore in an oogonium which lacks periplasm, and on these grounds the latter worker in particular postulated the origin of a Pythium-Peronosporaceae series from simple species through *Olpidiopsis*. Use of the terms antheridia and oogonia for the male and female thalli respectively in this genus is obviously open to serious question since these terms in their proper sense relate to gametangia which produce more or less differentiated gametes. Furthermore, in some species, i.e., *O. andréi*, the thalli which fuse may be equal in size, so that sexual reproduction is occasionally isogamous. Nevertheless, the development and evolution of antheridia and oogonia and the oomyctous type of sexual reproduction is clearly foreshadowed in *Olpidiopsis*. In the discussion which follows the non-committal terms male and female will be used for the thalli which fuse.

In the early developmental stages in living material, the female thalli are identical in appearance to those which are to develop into zoosporangia, and it is not until they have attained considerable size

that they can be distinguished. All thalli therefore appear to be potential zoosporangia and male or female thalli in the early developmental stages. This is strongly suggested by Maurizio's figure 7 of *O. major* which shows two male thalli attached to a larger female thallus with an aborted exit tube. The male thalli are indistinguishable from small young zoosporangia also except for their close association with the female thalli (fig. 54). In fixed and stained material, on the other hand, the female thalli can be recognized quite clearly by their staining reaction. Barrett found that they have a marked affinity for Orange G, while the zoosporangia and male thalli readily take up gentian violet. McLarty likewise noted that the female thalli may be distinguished in the young stages by numerous fatty bodies which stain brilliantly with crystal violet.

Successive developmental stages of a parthenogenetic and a sexual resting spore are shown in figures 55 to 58. In both of the incipient spores are numerous large refractive fatty globules, which later appear to decrease in size but increase in number. The endospore is well developed in figures 55 and 56, but in figure 53 there is yet no evidence of the exospore. Instead, the incipient spores are surrounded by hyaline or slightly amber-colored zones. The formation of the exospore usually first becomes evident as a homogeneous, amorphous layer which develops centripetally around the spores and gradually replaces the closely surrounding granular host protoplasm shown in figure 54. It is in this layer or zone apparently that the host protoplasm is transformed into spines, warts, knobs, or a smooth undulating layer. In *O. Pythii* (figs. 118-120) Butler reported that the host protoplasm condenses centripetally, so that at one period the outer ends of the spines appear sharp and fully formed while the proximal part is still enveloped in host protoplasm. The investing band of protoplasm described by Butler is probably a zone in which the host protoplasm is being transformed and deposited as spines. A resting spore of *O. Achlyae* in the process of exospore formation from fixed and stained material is shown in figure 59. The condensation or deposition appears to be occurring along radially oriented lines, and in certain regions the lines are localized and organized into conical groups or bundles, which apparently represent incipient spines. It is to be further noted that the lines do not extend all the way in, but are progressing from the outer margin toward the center. That the layer or zone shown in figure 55 is not merely a region filled with cell sap may be demonstrated by microdissection. McLarty found by such studies that this zone is a comparatively tough structural layer. After the spines have been fully formed the boundary of this layer may often persist as a thin membrane-like structure (figs. 56, 60) around the tips of the spines, which gives the impression that the resting spore lies in an empty hyaline vesicle. McLarty found that the exospore may be poorly developed in resting spores which use up most of the host protoplasm in the early developmental stages, and suggested that

the extent of exospore formation, i.e., length, thickness, and abundance of spines, warts, knobs, etc., is dependent on the amount of host protoplasm present at the time of its development. In that event, it will obviously vary to a high degree and is not to be regarded as a stable diagnostic character. Furthermore, the exospore composed of spines, warts, knobs, or a smooth undulating layer does not give a positive cellulose reaction when tested with chloro-iodide of zinc.

As noted above, the exospore may exhibit marked variations in a single species. In *O. Achlyae* it may be smooth, even, or undulating in contour (figs. 56, 61, 65, 66) as in *O. incrassata*; composed of fine, thread-like spines (fig. 64) as in *O. fibrillosa*; broad triangular spines, as in *O. minor* (figs. 60, 63, 67); long tapering curved spines (fig. 62) as in *O. curvispinosa*; or partly smooth and spiny (fig. 65). Occasionally, two resting spores and two male cells may be enveloped by one exospore (fig. 66). Parthenogenetic spores may vary in exospore structure to the same degree as the sexual spores in *O. Achlyae*. Similar but less extensive variations have been described by Shanor ('39a) for *O. varians*, and an examination of figures 91 to 111 shows how variable the earlier known species of *Olpidiopsis* also are. The empty male thalli or companion cells likewise may be smooth, echinulate, warty or spiny. Obviously, a character as variable as the exospore is of little diagnostic value in distinguishing species.

Returning to the description of plasmogamy and karyogamy, it is to be noted that the male and female thalli are multinucleate before they show any marked visible differentiation as gametes, except for relative size. Their nuclei may continue to divide mitotically (figs. 68-76) up to and even during (fig. 78) the initial stages of plasmogamy as has been shown by Barrett and McLarty. The first step in plasmogamy in species in which it occurs through a pore, according to Barrett, is a swelling and gelatinization of a portion of the intervening wall between the fusing thalli (fig. 77). In fixed and stained material this region is usually heavily stained. A more advanced stage of gelatinization is shown in figure 78 where the cell wall material appears to be diffusing into the two thalli. The nuclei in the male thallus are dividing while those in the female are at rest, but it is not uncommon to find them dividing in both gametes during plasmogamy. After the so-called fertilization pore has been formed the protoplasm of the male thallus begins to flow into the female (figs. 57, 79). The passage may be completed within a few minutes or last several hours. Following plasmogamy, the fused protoplasts change in their susceptibility to stains and have a greater affinity for safranin, according to Barrett. The gametic nuclei become irregularly distributed in groups and decrease considerably in size. At the same time the number of refractive oil globules increases, and the fertilization pore closes. During these processes the exospore undergoes differentiation, as described above, and attains its definitive

character. There are no size differences between the male and female nuclei, so that it is impossible to distinguish them on this basis, according to Barrett and McLarty. Both of these workers found nuclei in pairs, and Barrett figured a few stages of what he believed to be nuclear fusion (figs. 80-82). Although he did not find conclusive evidence of nuclear fusions in pairs, he nonetheless believed it occurs. McLarty, on the other hand, failed to observe fusion and held that the occasional occurrences of nuclei in pairs may be merely fortuitous. Therefore, the problem of the type of karyogamy, i.e., whether the numerous gametic nuclei fuse in pairs or all but one pair degenerate, in *Olpidiopsis* still remains to be solved. That plasmogamy of male and female thalli is not always essential to resting spore development is evident in the species which are partly or wholly parthenogenetic. In *O. Achlyae*, McLarty observed cases in which only part of the male protoplast passed into the female thallus. Occasionally one male may "serve" two female thalli, and in some instances as many as two to eight empty male thalli have been found attached to a single resting spore. Apparently in these instances there are supernumerary male nuclei following plasmogamy, but whether or not the unmated ones degenerate is not known. Obviously, sexual reproduction in *Olpidiopsis* presents numerous unsolved cytological problems, and until these have been solved it will be impossible to determine how closely *Olpidiopsis* is related to the higher Oomycetes.

It is also probable that male thalli are capable of developing androgenetically into resting spores. At least this is suggested by the small spore shown in figure 108. In some species the male thallus is attached to the female by an attenuated neck or canal (figs. 143, 144, 149, 150, 156), through which the male protoplast passes during plasmogamy. As in other organisms this neck is generally referred to as a conjugation or fertilization canal. Sometimes the male thalli may occur in tandem (fig. 149) but whether or not the content of the terminal one passes through the adjacent companion cells to reach the female in such cases is not known.

### Sex Determination

It has been generally assumed by most mycologists that species of *Olpidiopsis* are heterothallic, inasmuch as the resting spores are formed usually by fusion of thalli of unequal size. However, the monospore culture experiments of McLarty and Shanor on *O. Achlyae* and *O. varians* have discredited this belief, and it now seems that most, if not all, *Olpidiopsis* species are homothallic or haplosynoecious as was earlier suggested by the author ('39) and McLarty ('39b). As noted elsewhere McLarty and Shanor found that sexually formed resting spores may occur readily in cultures propagated from a single zoospore. Similar results will probably be secured from other species when they have been

studied in monospore cultures. In light of what is known to occur in haplonts, meiosis probably occurs during the first division of the diploid (?) nuclei in the germinating resting spore, but whether or not sex is genotypically differentiated at this stage is not absolutely certain inasmuch as McLarty and Shanor did not make monozoospore cultures from germinating resting spores. However, the fact that a single zoospore from a sporangium will give rise to cultures which later form male and female thalli shows that it carries the potentialities of both sexes. If sex is genotypically determined at meiosis in the germinating resting spore the resultant zoospores would be male and female in equal numbers and develop into sporangia of opposite sexes, which is contrary to the results obtained by McLarty and Shanor. According to their data sex in *Olpidiopsis* appears to be determined phenotypically at some stage in the haploid generation. *Olpidiopsis Achlyae* and *O. varians* accordingly seem to be haplosynoecious. At which stage in the life cycle sex differentiation occurs is not known. As has been pointed out above incipient zoosporangia as well as the male and female thalli are multinucleate and quite similar in appearance, and until differentiation occurs it is impossible to tell which type of reproductive structure is going to develop from them. It seems that all thalli in the early stages are potential male and female cells which under certain external environmental and internal conditions become differentiated and develop into gametes.

### Cellular Relations Between Host and Parasite

As has been noted elsewhere, all species of this genus appear at present to be obligate parasites with a limited host range. So far they have not been successfully grown on synthetic media, although Diehl ('35) was able to bring zoosporangia to maturity on agar. According to his observations, the maturation stages of zoosporangia are not dependent on the presence of the host. All *Olpidiopsis* species which parasitize members of the Saprolegniales and *Pythium* usually cause marked local hypertrophy of the infected hyphae but do not induce septation except in the case of *Pythium*. In the latter host the supporting hyphae may occasionally be delimited from the remainder of the mycelium by cross walls (figs. 112, 113). The swellings in the host hyphae may vary markedly in shape and size, and may be terminal, intercalary, or in some cases project out as lateral diverticula. Most species which parasitize algae cause little or no hypertrophy, but *O. zoppii* and *O. appendiculata* may induce local swellings which are two to four times the normal diameter of the algal filaments. Infection by *O. Oedognoriorum* leads to the formation of a conspicuous plug of cellulose by the host cell (fig. 131) at the point of entry of the germ tubes.

In cases of infection by *O. Achlyae*, the penetration of the germ tube and entrance of the parasite

may cause a localized temporary agitation of the host protoplasm, according to McLarty. The refractive granules in the latter swirl in eddies around the young parasite (fig. 10) and soon obscure it from view. This reaction, however, is of short duration, because when the parasite again becomes visible it is closely surrounded by the host protoplasm and hardly distinguishable from ordinary protoplasmic inclusions. The two protoplasts appear to be intimately associated, and no visible antagonism is exhibited. At least, there is no retraction of the host protoplasm away from the parasite. The host nuclei appear normal in its immediate vicinity and apparently are not stimulated to divide by its presence. In *O. schenkiana* (fig. 133), *O. Oedogoniorum*, and *O. andreei* (fig. 162), as noted before, the young parasite migrates toward and becomes closely applied to the host nucleus, and in the case of *O. andreei* (*P. Ectoearpii*) may completely engulf it.

As the thalli increase in size the free floating phase ends and the parasites become more or less localized in the hyphae. At this stage the host protoplasm begins to flow toward and accumulates around the thalli, and in a short time hypertrophy of the host begins. In some instances the swelling appears to be initiated in the immediate vicinity of the parasite, but this is not the general rule. Furthermore, hypertrophy does not invariably occur. In some oogonia and hyphae containing limited amounts of protoplasm McLarty found little or no distortion following infection by *O. Achlyae*. Accordingly, he believed that the swellings are not due to direct stimulation by the parasite but to the great accumulation of the host protoplasm in its immediate vicinity. That the host wall is stretched in such regions has been demonstrated by Dichl's ('35) plasmolytic experiments.

As the swellings increase in size conspicuous vacuoles appear in the host protoplasm (figs. 1, 54). These soon become traversed by more or less radiating strands of protoplasm moving slowly towards the parasite. This movement continues until all or most of the protoplasm has been attracted to and absorbed by the developing thalli. In the species which parasitize green algae the plastids and nuclei are destroyed, and at maturity the sporangia (fig. 146) and resting spores are partly surrounded by a mass of degenerated protoplasm. In *O. Ricciae* on *Riccia*, however, no harmful effects are apparent, according to du Plessis. This species occurs only in the rhizoids and basal swelling of the same, and although they become infected when young they develop normally. No distortion, swelling, rupture or necrotic effects are produced, and du Plessis accordingly believed that the relationship between host and fungus may possibly be symbiotic.

## PARASITES OF SAPROLEGNIA

**O. SAPROLEGNIAE** (Braun) Cornu, I.e., p. 145, Pl. 3, figs. 1-10.

*Chytridium Saprolegniae* Braun, 1855a, Ber. K'gl. Preuss Akad. wiss. 1855: 384, 1855b, Abh. K'gl. Akad. wiss. Berlin 1855: 61, Pl. 5, fig. 23.

*Olpidium Saprolegniae* Braun, I.e., p. 75.

*Diplophysa Saprolegniae* Schroeter, 1886, Cohn's Krypt'fl. Schlesiens 3: 195.

*Pseudolpidium Saprolegniae* Fischer (pro parte) 1892, Rabenhorst's Krypt'fl. I, 4: 35.

*Otpidiopsis echinata* Petersen, 1909, Bot. Tidsskr. 29: 405, Fig. XVIIa. 1910, Ann. Mycol. 8: 540, Fig. XVIIa.

Zoosporangia usually numerous in a host cell, hyaline, smooth or spiny (?), variable in size and shape, spherical, 15-150  $\mu$ , oval, 67  $\mu \times$  90-100  $\mu$ , ellipsoid and elongate 15-25  $\mu \times$  20-150  $\mu$ , with one to several short or elongate, straight, curved, or irregular exit tubes which end flush with the surface of the host cell or extend considerably beyond it. Zoospores isocont (?), oval, or slightly bean-shaped with the flagella attached near the anterior end. Resting spores parthenogenetic (?) or sexual, brown, oval spherical, 28-107  $\mu$ ; endospore thick, exospore covered with numerous short (?) spines; companion or male cells when present 1 to 4 per resting spore, hyaline, smooth, oval, spherical, 18-32  $\mu$ ; germination unknown.

Parasitic in *Saprolegnia* sp., *S. ferax*, *S. thureti*, and *S. mixta* in Germany [Nageli, '44 (?); Braun, '55a, '55b; Pringsheim, '60; Reinsch, '78 (?); Behla, '03; Minden, '11; Dichl, '35]; *Saprolegnia* sp., in France [Cornu, I.e.; Dangeard, '90; Varitchak, '31 (?)], Russia (Sorokin, '83, '89), Roumania (Constantineanu, '01); *S. dioica* and *S. monoica* in Denmark (Petersen, '09, '10); *S. thureti*, *S. declina*, *S. delicata*, *S. mixta*, *S. littoralis*, *S. monoica*, *Saprolegnia* sp., *Isoachlya anisospora*, *I. unispora*, and *I. eccentrica* in the U. S. A. (Barrett, '12; Davis, '14; Schwarze, '22; Harvey, '27, '42; Graff, '28; Maneval, '37; Shanor, '40; Couch, '41; Wolf, '41); *S. thureti* and *S. monilifera* in Japan (Tokunaga, '33) causing large terminal and intercalary swellings in the host hyphae.

According to Shanor, this species is limited in host range to species of *Saprolegnia* and *Isoachlya* and will not infect *Achlya*, *Aphanomyces*, *Aplanes*, *Dictyuchus*, *Leptolegnia* and *Protoachlya* species. If this is true, the parasites described by Petersen ('09, '10), Coker ('23), Gilman and Areher ('29) and Sparrow ('32, '33) as *O. Saprolegniae* in *Achlya* relate to another species, unless these workers were mistaken about the identity of the host plants. Sparrow ('33) was of the opinion that Coker's fungus is *O. luxurians*, but this seems unlikely since the latter species is confined to *Aphanomyces* hosts, according to Shanor ('40). Inasmuch as Coker interpreted *O. Saprolegniae* in the sense of Fischer ('92), it is not improbable that the species which he observed in *A. flagellata* and *A. imperfecta* may possibly be *O. fusiformis* or *O. varians*. In view of the fact that sporangium size and shape and the character of the exospore are no longer diagnostically specific, and in the light of Shanor's contentions that the species are restricted to certain hosts, it is

obviously impossible to determine which of the parasites described in the older literature relate to *O. Saprolegniae*.

*Olpidiopsis Saprolegniae* Cornu is the type species of the genus and probably the parasite which Pringsheim mistook for a developmental stage of *Saprolegnia*. Cornu limited the name *O. Saprolegniae* to *Saprolegnia*—inhabiting parasites the resting spores of which are covered with numerous fine spines, but Fischer ('92) included Cornu's species in *Pseudolpidium* and restricted the name *O. Saprolegniae* to a species with hemispherical or blunt, hyaline, up to 3  $\mu$  high, warts or pegs on the resting spores. Barrett interpreted *O. Saprolegniae* in the original sense of Cornu and created a new species, *O. vexans*, for the parasite with warty resting spores described by Fischer. Diehl and Shanor supported Barrett's interpretation, but Coker and Graff accepted Fischer's distinction. The present writer is following Barrett's interpretation of *O. Saprolegniae* to a certain degree but only temporarily until all species have been more critically studied. *Olpidiopsis Saprolegniae* Fischer and *O. vexans* Barrett are accordingly reduced to synonyms of *O. incrassata*. However, this does not completely solve the taxonomic problems involved nor greatly aid beginners in recognizing and distinguishing *Olpidiopsis* species. In the first place, *O. incrassata*, for instance, is supposedly characterized by resting spores with a wavy undulating exospore, and the introduction under this name of synonymous species, *O. Saprolegniae* Fischer and *O. vexans*, with warty or knobby resting spores destroys this distinction. On the other hand, McLarty ('41) has clearly shown that *O. Achlyae* also may form resting spores with a wavy undulating exospore (figs. 58, 61, 66), which obviously indicates that this character is not specific for *O. incrassata* alone. Furthermore, *O. Saprolegniae* Cornu, according to Shanor ('40), is limited to the same *Saprolegnia* and *Isoachlyta* hosts as *O. incrassata*, with the exception of *I. eccentrica*. Therefore, on the basis of host relationship there is no distinction between these two species. In view of the fact that sporangium size and shape, number and length of exit tubes, and the character of the exospore no longer appear to be constant for a species, and in the event that Shanor's host range results are confirmed, it may perhaps be taxonomically expedient to lump all reported *Saprolegnia* parasites, with the possible exception of *O. irregularis*, under the name of *O. Saprolegniae* Cornu. In that event, Cornu's species would have the following synonymy:

*Chytridium Saprolegniae* Braun, l.c.

*Olpidium Saprolegniae* Braun, l.c.

*Olpidiopsis incrassata* Cornu, l.c., p. 146.

*O. Saprolegniae* Fischer, l.c.

*O. major* Maurizio, 1895. Jahresber. Nat. Ges. Gräubündens 38: 15.

*O. echinata* Petersen, l.c.

*O. vexans* Barrett, 1912. Ann. Bot. 26: 231.

*Diplophysa Saprolegniae* Schroeter, l.c.

*Pseudolpidium Saprolegniae* Fischer, l.c.

*P. incrassatum* Fischer, l.c.

Such a classification is based entirely on host relationship, which is often a questionable criterion of distinction. Nevertheless, the author is inclined to agree at present with Petersen's view that *O. Saprolegniae* and *O. incrassata* may possibly be identical. The results of Shanor's cross inoculation experiments appear to be fairly conclusive, but the number of monospore infections which he made is quite small. It is not altogether improbable that more ex-

#### PLATE 11

Figs. 88 to 90. Germinated resting spore and zoospores of *O. varians*. Exit tube passing through empty male thallus. Shanor, l.c.

Figs. 91 to 93. Echinulate, knobby and spiny resting spores of *O. Saprolegniae*. Cornu, '72; Petersen, '09, '10; and Shanor, '39b, respectively.

Fig. 94. Resting spore of *O. echinata*. Petersen, '09, '10.

Figs. 95 to 97. Smooth resting spores with attached male thalli of *O. Saprolegniae* var. *laevis*. Coker, '23.

Fig. 98. Three parthenogenetic and one sexual resting spore of *O. incrassata* with broad undulating exospores. Cornu, l.c.

Fig. 99. Greatly enlarged resting spore of *O. major* with three male thalli. Maurizio, '95.

Figs. 100, 101. Echinulate and knobby resting spores of *O. vexans*. Barrett, l.c., and Shanor, '39b, respectively.

Figs. 102, 103. Irregular lobed zoosporangium and heterocont zoospores of *O. irregularis*. Constantineanu, '01.

Fig. 104. Fusiform zoosporangia of *O. fusiformis*. Petersen, '09, '10.

Fig. 105. Broad-spined resting spore of *O. fusiformis*. Cornu, l.c.

Fig. 106. Similar resting spore of *O. minor*. Sparrow, '32.

Fig. 107. Resting spore of *O. index* with echinulate male cell. Cornu, l.c.

Fig. 108. Large and small resting spore of *O. fusiformis* (?). Small spore may possibly be androgenetic. Coker, l.c.

Fig. 109. Resting spore of *O. spinosa* with spiny male cell. Tokunaga, '33.

Fig. 110. Knobby resting spore of *O. Aphanomyces*. Petersen, '09, '10.

Fig. 111. Spiny parthenogenetic resting spore of *O. Aphanomyces*. Whiffen, '42.

#### *O. Pythii*

(All figures after Butler, '07)

Fig. 112. Three sporangia in a swollen spherical hyphal tip; supporting hypha with a cross wall.

Fig. 113. Mature sporangium.

Fig. 114. Zoospores clustered at mouth of exit tubes.

Figs. 115, 116. Bean-shaped, isocont zoospores with refractive granules.

Fig. 117. Spiny, parthenogenetic resting spores.

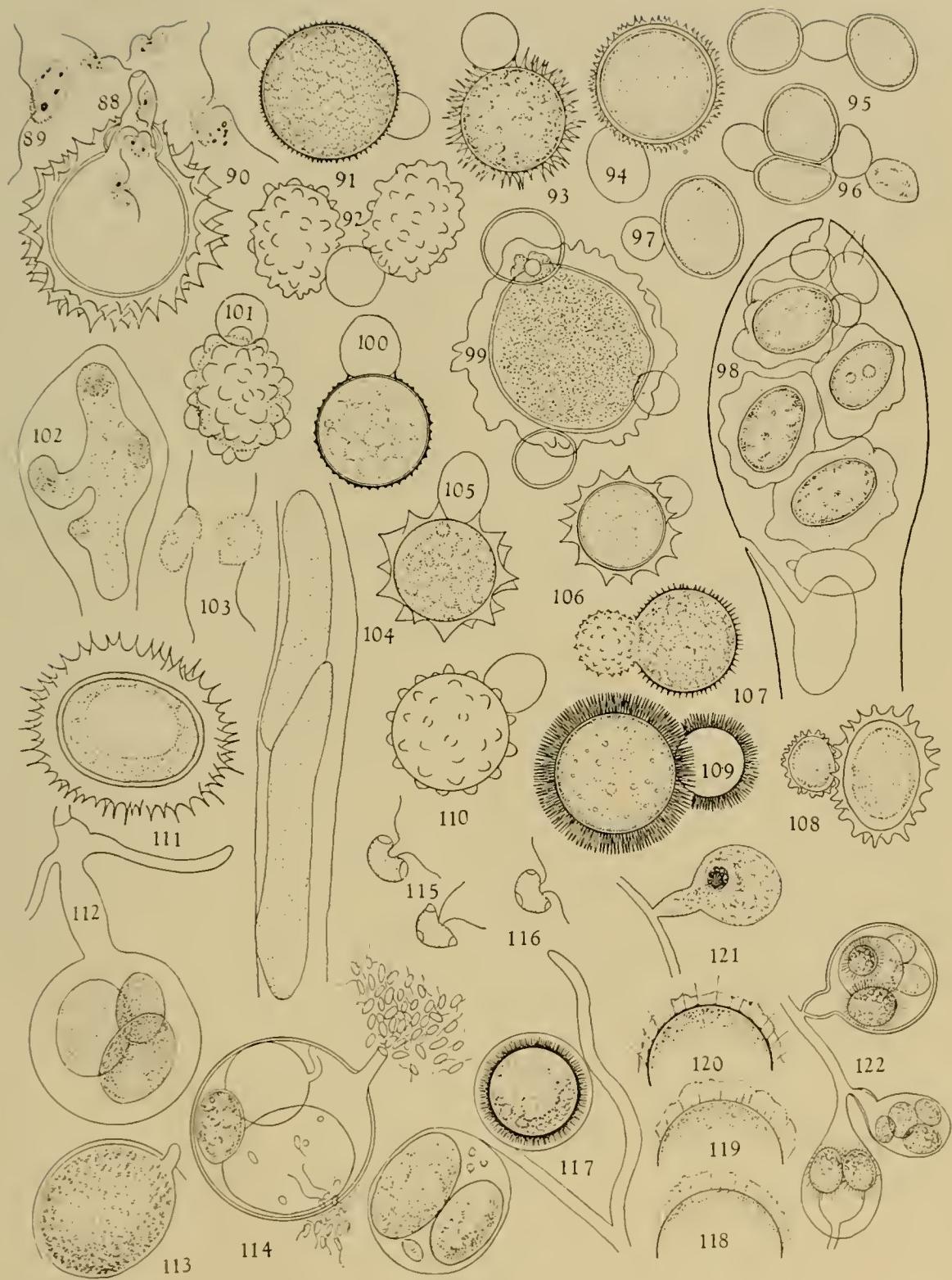
Figs. 118 to 120. Stages in the formation of spines on the resting spore.

#### *O. gracile*

Fig. 121. Young parasite in a swollen lateral diverticulum. Butler, l.c.

Fig. 122. Sporangia and resting spores in short swollen hyphal branches, Butler, l.c.

## PLATE 11



tensive tests under varying environmental conditions may produce different results.

Diehl made an intensive biological study of this species by growing its host under various cultural environmental conditions. He found that the young thalli may change their position in the galls regardless of the streaming of the host protoplasm and thus show independent amoeboid movement to some degree in the young stages of development. When infected hyphae of the host are transferred to agar the exit tubes of the parasite may grow out into filaments 200  $\mu$  to 567  $\mu$  long. Under such cultural conditions, the sporangia may mature and produce normal zoospores. Diehl has also found that resting spore formation occurs abundantly at low temperatures, and that 1 to 3 so-called male thalli may fuse with the larger female cell.

**O. SAPROLEGNIAE** var. *laevis* Coker, 1923. The Saprolegniaceae, p. 185. Pl. 62, figs. 1-6.

Zoosporangia solitary or up to seven in a cell, hyaline, smooth, spherical, oval, ellipsoid with 1-2 tapering exit tubes of variable length which project only slightly beyond the host cell. Zoospores small. Resting spores oval or elliptical, thick-walled and smooth; companion cells, 1-2, spherical, oval, elliptical, hyaline, and smooth; germination unknown.

Parasitic in *Saprolegnia ferox* and *S. monoica* in North Carolina, U. S. A.

**O. INCRASSATA** Cornu, l.c., p. 146, pl. 4, fig. 12.

*O. Saprolegniae* Fischer, l.c., pp. 34, 38.

*O. major* Maurizio, 1895. Jahresh. Nat. Ges. Graubündens 38: 15, figs. 4-9.

*O. vexans* Barrett, 1912. Ann. Bot. 26: 231.

*Pseudolpidium incrassatum* (Cornu) Fischer, l.c., p. 37.

Zoosporangia solitary or numerous, up to 12 or more in a host hypha, hyaline, smooth, or covered with spines of various lengths, thicknesses, and abundance; spherical, 20-176  $\mu$ , oval ellipsoid, 6-30  $\mu \times$  90-124  $\mu$ , or elongate with 1 to 7 straight or curved, coiled, stout or filamentous and occasionally branched exit tubes of varying lengths. Zoospores isocont. oval, ellipsoid and somewhat elongate, slightly flattened on one side; flagella attached near the anterior end. Resting spores parthenogenetic or sexual, spherical, 30-60  $\mu$ , oval, ellipsoid, 40-80  $\mu \times$  80-116  $\mu$ , rarely elongate, 5  $\times$  105  $\mu$ ; exospore dark greyish-brown, thin and warty, or thick, undulating and wavy in contour, hyaline (?), yellowish-brown or bright-golden in color; endospore fairly thin or thick; contents coarsely granular with one to several small or large refractive globules; companion or male cells when present 1 to 4 per resting spore, hyaline and smooth, spherical, 18-30  $\mu$ , oval, 15-20  $\times$  20-32  $\mu$ ; germination unknown.

Parasitic in *Achlya racemosa* (?) in France (Cornu, l.c.) and Denmark (Petersen, '09, '10); *Achlya* sp. (?) in Russia (Sorokin, '83, '89) and the U. S. A. (Sparrow, '33); *Saprolegnia thureti*, and *S. monoica* in Germany (Fischer, '92); *S. thureti*

and *S. hypogyna* in Switzerland (Maurizio, l.c.); *S. ferox*, *S. dielina*, *S. delica*, *S. mixta*, *S. monoica* (?), *S. littoralis*, *Isoachlya anisospora* and *I. unispora* in the U. S. A. (Barrett, l.c.; Shanor, '39, '40), causing large terminal clavate swellings in the host hyphae.

According to Cornu this species is characterized by resting spores with a yellowish-brown wavy or undulating exospore as is shown in figure 98. The inclusion, however, of other species with warty and knobby resting spore as synonyms of *O. incrassata* changes this original distinction, and it is now impossible to distinguish this species by the character of the exospore alone.

Maurizio's *O. major* (fig. 99) is apparently the same as *O. incrassata*, but whether or not Fischer's *O. Saprolegniae* and Barrett's *O. vexans* are identical to Cornu's species may be open to question. Shanor ('40) came to the conclusion that they are identical as a result of his cross inoculation experiments. As is shown in table 1, he found that *O. incrassata* is limited in host range to species of *Saprolegnia* and *Isoachlya* and will not infect *Achlya*. For this reason the present writer has inserted question marks after the *Achlya* species listed in the above host index. However, the number of Shanor's monozospore infections is quite small, but if the general conclusion to be drawn from his results are confirmed it is obvious that the reports of Cornu, Sorokin, Petersen and Sparrow that *O. incrassata* occurs in *Achlya* species are incorrect. Shanor held that Cornu was probably in error about the identity of his host plants, since no apparent attempt was made to obtain them in pure culture for accurate identification. Shanor further pointed out that infected hosts often became so distorted and atrophied that identification is impossible unless they are grown in pure culture. Whether or not Sorokin, Petersen, and Sparrow also were mistaken about their host plants is impossible to determine at present. On the other hand, the possible existence of biological races of *O. incrassata* which parasitize *Achlya* must not be ignored in discussions of the host range of this and other *Olpidiopsis* species. Sorokin saw only oblong zoosporangia and no resting spores, so that it is not certain that he was dealing with *O. incrassata*. Fischer ('92) believed that Sorokin's fungus relates to *O. fusiformis* (*P. fusiforme*) instead of to the former species. Sparrow observed nothing but ellipsoid resting spores with a hyaline undulating wall, which differs in color from the golden yellowish-brown exospore described by Cornu and Maurizio. As noted elsewhere, Petersen believed that *O. incrassata* (*P. incrassatum*) Cornu is identical to *O. Saprolegniae* (*P. Saprolegniae*) Fischer and listed it as a synonym of the latter species.

**O. IRREGULARIS** Constantineanu, 1901. Rev. Gen. Bot. 13: 373, figs. 76, 77.

Zoosporangia solitary or up to 15 in a hypha, hyaline, smooth, oval, elongate, lobed and very irregu-

lar, size unknown, with one or two short exit tubes which do not project beyond the surface of the host hypha. Zoospores heterocont, spherical 4.5–5  $\mu$  in diameter, or oval, hyaline with small refractive globules; with one short flagellum directed forward and the longer one backward in swimming; often lying quiescent in a mass at the mouth of the exit tube before becoming motile. Resting spores unknown.

Parasitic in *Saprolegnia* sp., occasionally in association with *Rozella septigena*, in Roumania (Constantineanu, l.c.) and Denmark (Sparrow, '34), causing large terminal clavate swellings in the host hyphae.

This species takes its name from the irregular shape (fig. 102) of the sporangia, but sporangium shape is obviously a questionable diagnostic character in parasites as variable as *Olpidiopsis* species. Constantineanu was doubtful about its identity because no resting spores were found, and he assigned it tentatively to *Olpidiopsis* as a new species. It differs from the other parasites in *Saprolegnia*, as far as they are now known, by heterocont zoospores. As noted above, *O. irregularis* may be associated with *R. septigena*, and Constantineanu was of the opinion that it feeds of the latter's thallus.

## PARASITES OF ACHLYA

### *O. FUSIFORMIS* Cornu, l.c., p. 147, pl. 4, figs. 1–4.

*O. minor* Fischer, l.c., p. 39.

*Pseudotpidium fusiforme* Fischer, l.c., p. 37.

Zoosporangia solitary or numerous, smooth or spiny, elongate, fusiform, 26–78  $\mu \times$  98–350  $\mu$ , oval, 7–10  $\mu \times$  21.7–80  $\mu \times$  120  $\mu$ , spherical, 10–120  $\mu$ , with 1 to 3 exit tubes. Zoospores isocont (?) egg-shaped, oval, slightly elongate, 2  $\times$  4  $\mu$ . Resting spores parthenogenetic or sexual, solitary or numerous, yellowish-brown, spherical, 30–60  $\mu$ , covered with fine short, or broadly conical and triangular spines up to 10.5  $\mu$  in height; contents coarsely granular with one to several refractive globules; companion or male cells when present 1 to 3 per resting spore, hyaline and smooth, oval, spherical 16–24  $\mu$ ; germination unknown.

Parasitic in *Achlya leucosperma*, *A. racemosa* and *Achlya* sp., in France (Cornu, l.c.); *A. flagellata*, *A. leucosperma*, *A. racemosa* and *A. polyandra* in Germany [Cienkowski, '55 (?); Reinsch, '78 (?); Fischer, '82, '92; Minden, '11]; *Achlya* sp., and *Saprolegnia* sp. (?), in Russia (Sorokin, '83, '89); *Achlya* sp., in Denmark (Petersen, '09, '10); *A. flagellata* and *A. flagellata* var. *yezoensis* and *A. racemosa* in Formosa and Japan (Sawada, '16, '19; Tokunaga, '33); *Achlya* sp., *A. flagellata*, *A. racemosa*, *A. imperfecta*, *A. klebsiana*, and *Saprolegnia* sp. (?) in the U. S. A. (Sparrow, '32; Matthews, '35; Shanor, '39, '40); *Achlya* sp., in England (Sparrow, '36), and *A. racemosa* in Czechoslovakia (Cejp, '34), causing large terminal and intercalary fusiform and clavate swellings in the host hyphae.

This species was named *fusiformis* by Cornu because of the fusiform, elongate, and almost linear shape of its zoosporangia. This character, however, is not very specific, since fusiform and greatly elongate zoosporangia have been reported in other species as well. Furthermore, resting spores with broad triangular hyaline spines, which are reported to be characteristic of *O. fusiformis*, may occur in *O. Achlyae* and *O. varians* also.

Shanor ('40) found that *O. fusiformis* is limited in host range to *A. racemosa* and *A. imperfecta* and will not infect the other *Achlya* species which he tested (table 1). Particularly noteworthy is the fact that it did not infect *A. flagellata*, although seven infection attempts were made. These results contradict the reports of Sawada, Tokunaga, and Matthews of its occurrence in this host. *Achlya imperfecta* and *A. klebsiana* were heavily parasitized, but *A. racemosa* was infected only slightly in Shanor's experiments.

Sorokin and Sparrow are the only two workers who have reported *O. fusiformis* in *Saprolegnia*, and here again it is possible that they were mistaken about the identity of the host plants. On the other hand, they may equally well have had *O. Saprolegniae* or *O. incrassata* at hand. Sparrow believed that the fungus which Petersen reported as *O. fusiformis* relates to *O. Aphanomyces* (*O. luxurians*), but this is unlikely inasmuch as the latter species is limited in host range to *Aphanomyces*.

As has been pointed out elsewhere, the parasite of *A. imperfecta* and *A. flagellata* which Coker ('23) described as *O. Saprolegniae* Fischer may possibly relate to *O. fusiformis* or *O. varians*, or in part to both species.

Whether *O. index* (Cornu) l.c., p. 145, pl. 3, (fig. 11) is a valid species or identical to *O. fusiformis* is not certain. Cornu described it as a parasite of *Achlya* sp., usually with solitary, very large elliptical zoosporangia and resting spores and echinulate companion cells (fig. 107). No measurements were given of the size of the sporangia, zoospores, and resting spores. The presence of echinulate companion cells was nevertheless regarded by Cornu as specific, and he accordingly diagnosed the parasite as a distinct species. However, it is very doubtful that the occurrence of echinulations and spines on the companion cells is a specific character, since both smooth and spiny male cells have been reported in *O. varians*, *O. curvispinosa*, and *O. brevispinosa*.

*Olpidiopsis spinosa* (Tokunaga, '33, Trans. Sapporo Nat. Hist. Soc. 13: 25, Pl. 2, figs. 10–11) parasitizes *A. flagellata* and occurs in association with *O. fusiformis* and *O. minor* in Japan. Tokunaga described it as follows: Zoosporangia solitary or numerous, hyaline, smooth, ellipsoid, elongate or cylindrical, 34–61  $\mu \times$  92–198  $\mu$ , with one or two exit tubes; zoospores isocont, ellipsoid or elongate, size unknown, with the flagella attached laterally near the anterior end; resting spores hyaline, spherical, 51–73  $\mu$ , covered with numerous fine, 9.6  $\mu$  long spines; germination unknown; companion cells sin-

glc, hyaline, globose,  $25.2 \mu$ – $32.4 \mu$ , covered with numerous fine spines.

The size and shape of the sporangia of this species are strikingly similar to those of *O. fusiformis*, and besides the presence of long, fine spines on the companion cells (fig. 109) there are few or no characters to distinguish it from the latter species. While the spines on the resting spores of *O. fusiformis* and *O. minor* are reported to be broad and triangular, it is not improbable that they vary considerably in thickness, shape and length and may attain the dimensions of those described by Tokunaga. The present writer is accordingly inclined at present to regard *O. spinosa* as a synonym of *O. fusiformis*.

It is quite possible that *Pseudolpidium stellatum* (Sawada, 1912. Spec. Bull. Agr. Expt. Sta. Formosa, 3: 70, pl. 8, figs. 11–16) is synonymous with this species also. Sawada found this species in *A. prolifera* in 1912 and 1919 in Japan, and it was subsequently reported by Tokunaga in 1933. Zoosporangia and zoospore were not observed, and the resting spores were reported to be hyaline, spherical, ovoid, or globoid,  $24$ – $100 \mu$ , and covered with long  $9$ – $24 \mu$ , pointed and sharp spines. No male or companion cells were found. Sawada reported that *P. stellatum* may occur independently or in association with *O. fusiformis*.

**O. VARIANS** Shanor, 1939. Jour. Elisha Mitchell Sci. Soc. 55: 171. Pl. 24.

Zoosporangia solitary or numerous, smooth, warty or spiny, spines up to  $7 \mu$  in length, spherical, oval, ellipsoid,  $40$ – $140 \mu$  by  $60$ – $350 \mu$ , frequently  $80 \times 200 \mu$ , with 1 to 5 exit tubes. Zoospores isocont, oval to elongate,  $2.3$ – $3 \mu \times 3.8$ – $4.6 \mu$ ; flagella  $4.2$  to  $4.6 \mu$  long. Resting spores yellowish-brown, spherical  $26$ – $83 \mu$ ; exospore hyaline to yellowish in color,  $1.2 \mu$  thick, usually bearing coarse, abruptly-tapering spines,  $8.6 \mu$  high, which are connected by a reticulum; endospore yellowish-brown,  $1.7 \mu$  thick; companion or male cells 1 to 2 per resting spore, usually spherical,  $17$  to  $30 \mu$ , occasionally smooth, usually enveloped by the spiny exospore of the resting spores, spines  $1.7 \mu$  long; resting spore transformed directly into a zoosporangium in germination with an exit tube which usually penetrates the companion cell.

Parasitic in *Achlya flagellata*, *A. racemosa*, *A. colorata* and *A. proliferoides* in North Carolina, U. S. A. (Shanor, '39a, '39b, '40) causing large terminal or intercalary swellings in the host hyphae.

Shanor found that this species is limited to the *Achlya* species listed above and will not infect *A. americana*, *A. imperfecta*, *A. klebsiana*, *A. recurva*, *A. apiculata*, *A. glomerata*, nor any of the species of *Saprolegnia*, *Aplanes*, *Protoachlya*, *Isoachlya*, *Aphanomyces*, *Dictyuchus*, and *Leptolegnia* shown in table 1. This species is highly variable in sporangium size and shape as well as in the character of the exospore, and was named *varians* because of its variability. The spines are broad and triangular as

in some specimens of *O. fusiformis* and *O. Achlyae* (figs. 86, 87), and some of the resting spores are strikingly similar to those of *O. minor* (fig. 106). Furthermore, the companion cells are usually enveloped by the spiny exospore of the resting spore, although the spines in the vicinity of such cells are usually shorter. A similar envelopment has been shown to occur in *O. Achlyae* (fig. 66).

**O. ACHLYAE** McLarty (ad int.) 1941a. Bull. Torrey Bot. Club, 68: 62, figs. 1–26. 1941b. Ibid. 68: 75, figs. 1–80.

Zoosporangia solitary or up to 50 in a hypha, smooth or covered with fine or coarse noncellulosic spines or bristles, variable in size and shape, spherical, oval, ellipsoid or elongate,  $13.2$ – $112.4 \times 115$ – $666.4 \mu$ , with 1 to 3 exit tubes which may extend considerably beyond the surface of the host filament. Zoospores hyaline with numerous small refringent granules, oval or somewhat reniform  $2.3$ – $2.9 \mu \times 4.3$ – $5.7 \mu$ , usually about  $3.1 \times 4.2 \mu$ , with two approximately equal flagella attached laterally near the anterior end. Resting spores parthenogenetic or sexual, spherical or oval,  $22.8$ – $122.4 \mu$ , usually  $41 \times 50 \mu$ , brown, with several or usually one large refringent globule; endospore smooth cellulosic, 1 to  $1.5 \mu$  thick; exospore noncellulosic, 1 to  $11.4 \mu$  thick, covered with warty protuberances, small or large, narrow or broad-based spines, hair-like fibrillae, or with an entire, undulant or slightly serrate margin; companion or male cells 1 to 3 per resting spore when present, thin-walled, hyaline, smooth, sometimes embedded in the exospore, oval or spherical; resting spore transformed directly into a zoosporangium with an exit tube in germination.

Parasitic in *Achlya flagellata*, London, Ontario, Canada (McLarty, '39, '40, '41), causing large terminal and intercalary swellings in the host hyphae.

McLarty diagnosed this parasite temporarily as a new species, until the other *Olpidiopsis* species with which it appears to be identical have been more intensively studied. As is shown in Plates 9 and 10, it is highly variable in structure and may produce resting spores with exospores which are characteristic of most species of this genus. In general it resembles *O. fusiformis* most closely, so that the writer and his student, McLarty, were inclined to regard it as closely related or identical to this species. But if Shanor's data that *O. fusiformis* will not infect *A. flagellata* are correct, these two species are different in host range at least. Since *O. Achlyae* occurs on the same host and shows much the same variations as *O. varians*, it is possibly identical to the latter species. Although spiny companion cells have not been observed in *O. Achlyae*, this does not exclude the possibility of its being the same as *O. varians*. On the other hand, it is equally probable that *O. varians*, *O. Achlyae* and possibly *O. index* and *O. spinosa* may be biological varieties or races of *O. fusiformis* which are limited to particular hosts. If this proves

to be true, all *Achlya*-inhabiting parasites may possibly be grouped as a single species with several possible physiological races or varieties. To determine this possibility an intensive study of the degree of morphological variation of all species and their host range must be made.

## PARASITE OF APHANOMYCES

**O. APHANOMYCIS** Cornu, l.c., p. 118, pl. 4, figs. 5-11.  
*Pseudolpidium Aphanomyces* Fischer, l.c., p. 37.  
*O. tuzerians* Barrett, l.c., p. 231, Pl. 23, figs. 1, 5, 6, 9-14, 16-18, 21b-23; pl. 24, figs. 24-26, 28-31; pl. 25, figs. 43-46; pl. 26.

Zoosporangia solitary or numerous, up to 20 or more in a hypha, smooth, or spiny, spherical, oval, fusiform and elongate, dimensions unknown; one to several exit tubes which may extend considerably beyond the surface of the host cell. Zoospores isocont, oval, egg- and slightly bean-shaped, size unknown; coming to rest in a mass at the mouth of the exit tube for a few minutes and then swimming away; flagella inserted at (?) or near the anterior end. Resting spores parthenogenetic or sexual, brown, oval, spherical, 25-50  $\mu$ ; endospore thick, exospore comparatively thin and covered with conical spines, 2.5  $\mu$  in height, or blunt warts; contents granular with one or more large refractive globules; companion or male cells when present 1 to 3 per resting spore, hyaline, smooth, oval, ellipsoid, spherical, 10-25  $\mu$ , germination unknown.

Parasitic in *Aphanomyces* sp. and *Pythium* sp. (?) in France (Cornu, l.c.; Dangeard, '90); *Aphanomyces* sp., in Denmark (Petersen, '03, '09, '10) and Germany (Minden, '11); *A. laevis* in India (Butler, '07; Sydow and Butler, '07; Butler and Bishy, '31) and the U. S. A. (Barrett, l.c.; Shanor, '39, '40) and *A. cladogamous* (Whiffen, '42) causing large broadly fusiform intercalary and almost spherical terminal swellings in the host hyphae.

As noted above, Dangeard reported this species as a parasite of *Pythium*, but Butler ('07) and Shanor were unable to secure infection of *P. monospermum*, *P. proliferum*, *P. gracile*, and *P. aphaniidermatum* with it. Butler nevertheless believed that the resting spore figured by Dangeard relates to *O. Aphanomyces*, but as Minden ('11) and Shanor ('39) suggested it is probably the resting spore of *O. (Pseudolpidium) Pythii*. Shanor ('40) was unable to transfer *O. Aphanomyces* to *Aphanomyces stellatus*, *Achlya*, *Saprolegnia* and other water molds, and concluded that it is limited in host range to *Aphanomyces laevis*. Miss Whiffen, however, reported its occurrence in *A. cladogamous*. It is to be noted, however, that her fungus did not infect *A. laevis*, which suggests at once that it may be a physiological race of *O. Aphanomyces*. This remains to be shown, however, from more extensive cross inoculation experiments involving *Saprolegnia*, *Achlya* and other similar host species.

## PARASITES OF PYTHIUM

### O. PYTHII (Butler) comb. nov.

*Pseudolpidium Pythii* Butler, 1907, Mem. Dept. Agric. India, Bot. Ser. 1 No. 5:127, Pl. 7, figs. 9-16.

Zoosporangia solitary or numerous, hyaline, smooth, oval, and ellipsoid, up to 35  $\mu$  in the greatest diameter, with a single exit tube of varying length which extends for a short distance beyond the surface of the host. Zoospores isocont, hyaline, unequilateral, somewhat kidney-shaped with one to several small refractive granules; flagella laterally inserted; swarming in the vicinity of the exit canal for a brief period, then coming to rest for a few minutes in a dense cluster; finally swimming away slowly. Resting spores parthenogenetic, solitary or numerous, often in association with zoosporangia, oval or spherical, 19.2-30  $\mu$ , brown, comparatively thin-walled and covered with fine, thread-like, short, evenly spaced spines; germination unknown; companion or male cells lacking.

Parasitic in *Pythium monospermum*, *P. rostratum*, *P. vexans*, and *P. intermedium* in France (Butler, l.c.), *Pythium* sp., in Germany (Minden, '11), *P. oryzae* in Japan (Tokunaga, '33), and *Pythium* sp., in England (Sparrow, '36), causing oval, spherical, obpyriform or balloon-shaped enlargements at the end of the host hyphae or in lateral diverticula, and occasionally leading to septation of the hyphae.

### O. GRACILE (Butler) comb. nov.

*P. gracile* Butler, l.c., p. 129, pl. 7, figs. 1-8.

Zoosporangia solitary or numerous, up to 40 in a single swelling, hyaline, smooth or spiny, spherical, 4-52  $\mu$ , with 1 to 5 contorted and swollen exit tubes of varying lengths which may project considerably beyond the surface of the host cell. Zoospores, isocont (?), hyaline, obovate, elongate, and somewhat curved with one to several minute refractive granules, size unknown; one flagellum inserted near the anterior end, the other laterally; swimming motion smooth, body of spore often revolving on its long axis. Resting spores parthenogenetic, single or numerous, occurring in association with the zoosporangia, spherical to oval, 12-27  $\mu$  exclusive of spines, yellowish, containing a large refractive globule surrounded by a peripheral layer of vacuolate protoplasm; endospore .7 to 1.2  $\mu$  thick, exospore 1.7 to 2.5  $\mu$  thick and covered with long, 4  $\mu$ , tapering, thick, crowded spines; germination unknown; companion or male cells lacking.

Parasitic in *Pythium intermedium* in France (Butler, l.c.) and *P. rostratum* in the U. S. A. (Whiffen, '42) causing terminal enlargements and lateral, oval- or balloon-shaped diverticula in the host hyphae which may be 80-90  $\mu$  in their greatest diameter.

Whether the zoospores are heterocont or isocont is not certain from Butler's description. He reported that one flagellum is inserted near the anterior end while the second one is lateral, but his figure (fig.

12) suggests that they are both lateral in position. According to Miss Whiffen, *O. gracile* will not infect *P. torulosum*, *P. pulchrum*, *P. proliferum* nor the unidentified *Pythium* hosts of *O. brevispinosa* and *O. curvispinosa*.

**O. CURVISPINOSA** Whiffen, 1942. Amer. Jour. Bot. 29:610. Figs. 1, 5, 21.

Zoosporangia solitary or numerous, spherical to oval, 12–68  $\mu$  in greatest diameter, hyaline, smooth or covered by short bristles, with one to three exit tubes. Zoospores with numerous oil globules, elongate and somewhat reniform, size unknown; flagella of about equal length and attached near anterior end. Resting spores hyaline, spherical to oval, 17–24  $\mu$ , containing a large refractive globule surrounded by vacuolate protoplasm; exospore covered by curved spines up to 5  $\mu$  in length. Companion or male cell consistently present, hyaline, spherical, or oval, 14–20  $\mu$ , smooth or with short, closely-set spines; germination unknown.

Parasitic in *Pythium* sp., and *P. torulosum* in North Carolina, U. S. A., causing large terminal or intercalary swellings in the host hyphae.

**O. BREVISPINOSA** Whiffen, l.c., p. 610. Figs. 2, 22, 27.

Zoosporangia solitary or numerous, oval, spherical, 10.6–68.4  $\mu$ , with one to three exit tubes. Zoospores elongate and somewhat reniform with several oil globules; flagella of about equal length and attached near the anterior end. Resting spores dark brown, spherical to oval, 10.6–45.1  $\mu$ , containing a large refractive globule surrounded by vacuolate protoplasm; exospore 1.7–2.5  $\mu$  thick, covered by short, fine spines up to 3.5  $\mu$  in length, endospore .75–1.32  $\mu$  thick; companion cell consistently present, oval, spherical, 7.1–25.5  $\mu$ , smooth or spiny; germination unknown.

Parasitic in *Pythium* sp., from Louisiana, U. S. A., causing large terminal and intercalary swellings, up to 125  $\mu$  in diameter, in the host hyphae.

This species is limited in host range to an unidentified species of *Pythium* and will not infect *P. rostratum* nor the host of *O. curvispinosa*, according to Miss Whiffen's cross inoculation experiments.

## PARASITES OF ALGAE

**O. SCHENKIANA** Zopf, 1884. Nova Acta Ksl. Leop.-Carol. Deut. Akad. Nat. 47: 168. Pl. 15, figs. 1–32.

*Pleocystidium parasiticum* Fisch, 1884. Sitzb. Phys.-Med. Soc. Erlangen 16: 60. Figs. 24–39.

*Olpidiopsis parasitica* (Fisch) Fischer, 1892. Rabenh.-horst's Krypt'fl. I, 4: 40.

*Diplophysa schenkiana* (Zopf) Schroeter, 1897. Engler und Prantl, Die Nat. Pflanzenf. I, 1: 85.

*Pseudolpidiopsis schenkiana* (Zopf) Minden, 1911. Krypt'fl. Mark Brandenburg 5: 257.

*P. parasitica* (Fisch) Minden, l.c., p. 258.

Zoosporangia solitary or numerous, hyaline, smooth, spherical, oval, ellipsoid, egg-shaped, elongate, 21.6–26.4  $\mu \times$  30–81.6  $\mu$ , with one or two stout, short or elongate, up to 60  $\mu$  long, straight or

## PLATE 12

*O. gracile*

Fig. 123. Mature zoosporangium with 4 exit tubes; accompanied by a resting spore. Butler, l.c.

Figs. 124, 125. Pyriform heterocont (?) zoospores with refractive bodies. Butler, l.c.

Fig. 126. A large diverticulum with numerous sporangia and resting spores. Butler, l.c.

Fig. 127. Smooth-walled resting spore. Whiffen, '42.

*O. curvispinosa* and *O. brevispinosa*

Fig. 128. Resting spore of *O. curvispinosa* with long curved spines. Male cell spiny. Whiffen, l.c.

Fig. 129. Spiny resting spore and male cell of *O. brevispinosa*. Whiffen, l.c.

*O. schenkiana*

Fig. 130. Infection of *Spirogyra* cell. Zopf, '84.

Fig. 131. Cellulose plug on cell wall at point of entry of germ tube. Scherffel, '25.

Fig. 132. Forked germ tube, and young naked vacuolate parasite in host cell. Scherffel, l.c.

Fig. 133. Young parasite next to larger host nucleus (*P. parasiticum*). Fisch, '84.

Figs. 134 to 136. Zoosporangia and emission of zoospores. Zopf, l.c.

Fig. 137. A flagellate amoeboid primary swarmer with contractile vacuole. Scherffel, l.c.

Fig. 138. Side view of pyriform, heterocont secondary swarmer with contractile vacuole. Scherffel, l.c.

Figs. 139, 140. Optical and cross-section views of same. Scherffel, l.c.

Fig. 141. Early stage in resting spore formation. Zopf, l.c.

Fig. 142. Resting spore with one companion cell. Zopf, l.c.

Fig. 143. Resting spore with four companion cells. De Wildeman, '96.

Fig. 144. Similar resting spore (*P. parasiticum*) Fisch, l.c.

Fig. 145. Germination. Only one flagellum shown on zoospores. Zopf, l.c.

Figs. 146 to 148. Zoosporangium and resting spores of *O. zoppii*. De Wildeman, l.c.

Fig. 149. Resting spore of *O. fibrillosa*. Spines not shown. Two male cells in tandem. De Wildeman, l.c.

Fig. 150. Same with fibril-like spines. De Wildeman, l.c.

Fig. 151. Resting spore of *O. appendiculata*. De Wildeman, l.c.

*O. Oedogoniiorum*

(All figures after Scherffel, '25)

Fig. 152. Mature vacuolate zoosporangium.

Fig. 153. Isocont primary swarmer.

Fig. 154. Cystospores.

Figs. 155, 156. Resting spores in elongate hyaline vesicles with attached companion cells.

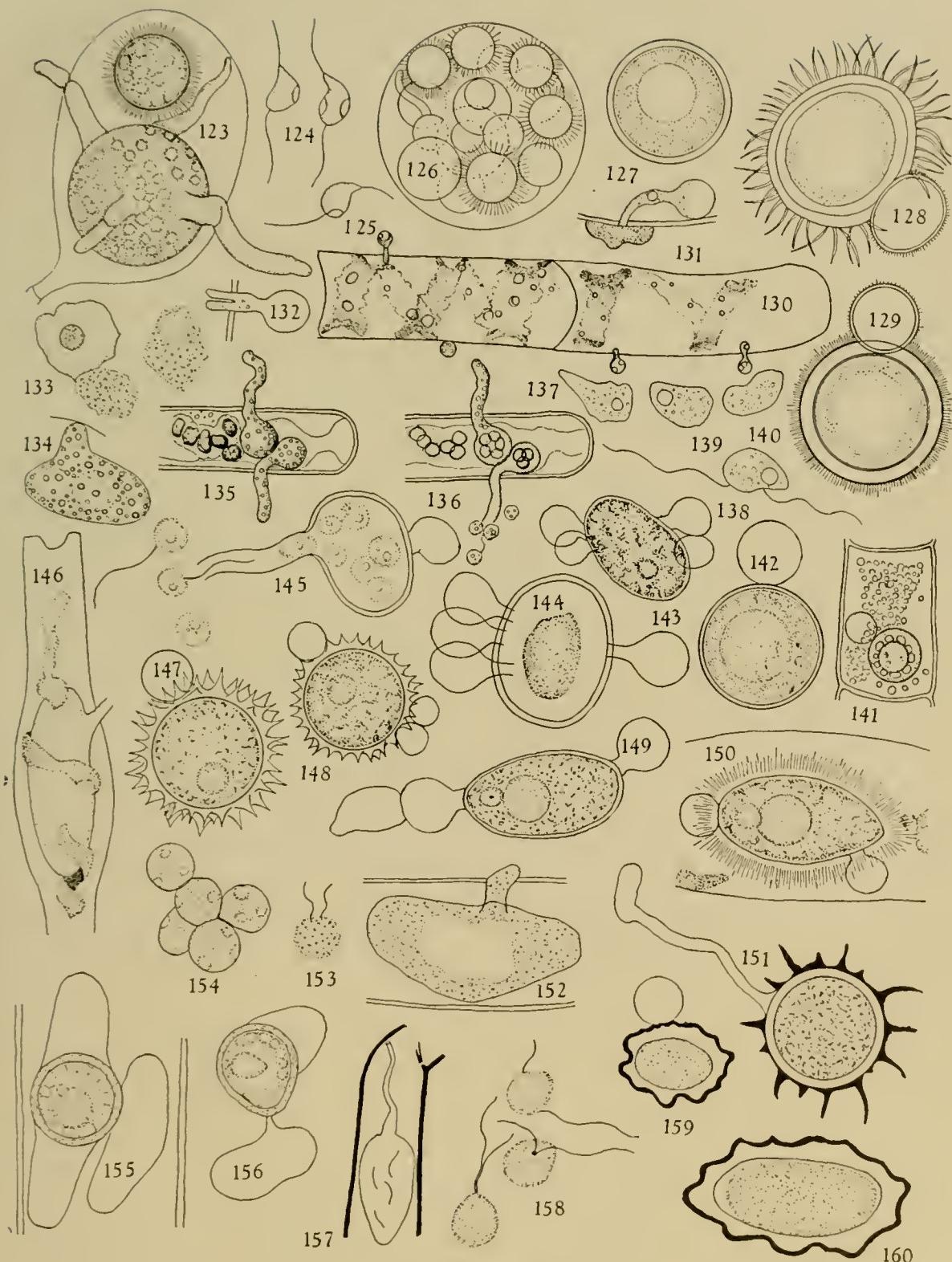
*O. Ricciae*

Fig. 157. Empty zoosporangium in a rhizoid.

Fig. 158. Anteriorly biflagellate, heterocont zoospores.

Figs. 159, 160. Resting spore with companion cell, and elongate parthenogenetic (?) spore.

## PLATE 12



curved exit tubes which may project considerably beyond the surface of the host cell or extend through adjacent cells. Zoospores heteroont, oval, pyriform,  $4 \times 6 \mu$ , and slightly bean-shaped; hyaline with several small refractive granules and a contractile vacuole; emerging singly, fully developed, and swimming directly away, or emerging and lying in a mass for a few minutes at the mouth of the exit tube before becoming amoeboid and flagellate and swimming away; flagella lateral (?), shorter flagellum extending forward and the longer one backward in swimming. Resting spores hyaline, smooth, oval, egg-shaped or spherical,  $30-40 \mu$ , thick-walled with a large refractive globule; companion or male cells 1 to 5 in number, hyaline, smooth, oval or spherical,  $16.8-21.6 \mu$ ; resting spore transformed directly into a zoosporangium with an exit tube in germination.

Parasitic in *Spirogyra* sp., *Mougeotia* sp., and *Mesocarpus* sp., in Germany (Zopf, l.e.; Fiseh, l.e.; Minden, '11); *Spirogyra* sp., in Hungary (Scherffel, '25); *Spirogyra* sp., in Belgium (de Wildeman, '90, '91, '96), Roumania (Constantinianu, '01), India (Butler, '07; Butler and Bisby, '31), Japan (Tokunaga, '33), causing no or only slight hypertrophy of the host cell. The writer also has frequently observed this parasite in *Spirogyra* sp., in the vicinity of New York.

Fiseh and Zopf, among the early workers, described the zoospores as uniflagellate, and for this reason Minden included this species in his new genus, *Pseudolpidiopsis*. Scherffel's observations, however, leave no doubt about the number of flagella, and Zopf's species may now be returned to the genus *Olpidiopsis*. Obviously the previous investigators had failed to observe the second flagellum. Fiseh's *Pleocystidium parasiticum* is included here as a synonym of Zopf's species, since it occurs in the same host and appears to have the same structure and type of development. Fiseh and Minden regarded both species as distinct because of the presence of up to five companion cells on the resting spores of *P. parasiticum*, but de Wildeman found up to four male cells per resting spore in *O. schenkiana* also. In view of the variations which Maurizio, Barrett, Diehl, McLarty, Shanor and others have observed in other species of *Olpidiopsis*, the number of companion cells present is a questionable diagnostic character.

#### **O. ELLIPTICA** (Schroeter) Fischer, l.e., p. 41.

*Diphysa elliptica* Schroeter, 1886. Cohn's Kryptofl. Schlesiens 3: 196.  
*Pseudolpidiopsis elliptica* (Schroeter) Minden, l.e., p. 260.

Zoosporangia and zoospores unknown. Resting spore obliquely ellipsoid, slightly less in diameter than the host cell, and covered with fine, scattered spines; companion or male cells slightly smaller than the spores, brown and smooth; germination unknown.

Parasitic in *Mesocarpus* sp., in Germany.

This species has been reported only once, but it is not altogether improbable that other species described from *Mesocarpus* may be identical or closely related to it. It is reported to differ from *O. schenkiana* chiefly by the presence of spines on the resting spores.

#### **O. SOROKINII** de Wildeman, 1890. Ann. Soc. Belge Micro. 14: 22, fig. 7.

Zoosporangia solitary, hyaline, smooth, elongate, sac-like or cylindric with a single short exit tube which ends flush with the surface of the host cell. Zoospores small. Resting spore unknown.

Parasitic in *Tribonema* (*Conferva*) *bombycinum* in Belgium.

This is a very doubtful species which de Wildeman thought might be identical to *O. fusiformis* var. *Oedogoniarum* Sorokin. Later in his Census Chytridinae ('96), however, he listed it as *Olpidium sorokinii*. Inasmuch as the resting spores are unknown its validity as a member of *Olpidiopsis* is very questionable.

#### **O. ZOPFII** de Wildeman, 1895. La Notarisia 10: 34. 1896, Ann. Soc. Belge Micro. 20: 25, pl. 1, figs. 1-3, 5-7.

*Pseudolpidiopsis zopfii* (de Wildeman) Minden, l.e., p. 259.

Zoosporangia solitary or numerous, hyaline, smooth, spherical, egg-shaped or ellipsoid with a single exit tube of varying length which usually projects beyond the surface of the host cell. Zoospores unknown. Resting spores spherical,  $16-22 \mu$ , with one or more refractive globules, thick-walled and covered with numerous stout, broad-based, abruptly tapering spines; companion cells 1 to 3 in number, small, oval, spherical,  $12 \mu$ , smooth, hyaline; germination unknown.

Parasitic in *Spirogyra* sp., in Luxembourg, causing local swellings, up to twice the normal diameter of the filaments.

#### **O. FIBRILLOSA** de Wildeman, 1895. l.e., p. 34. 1896.

Ann. Soc. Belge Micro. 20: 27. Pl. 2, figs. 13, 14, 18, 19.  
*Pseudolpidiopsis fibrillosa* (de Wildeman) Minden, l.e., p. 259.

Zoosporangia solitary, hyaline, smooth, oval or ellipsoid, with a single exit tube more or less broadened at the base. Zoospores unknown. Resting spores hyaline, thick-walled, spherical,  $20-25 \mu$ , oval, egg-shaped and ellipsoid with one to several refractive globules; exospore profusely covered with fine, radially oriented hair-like spines or fibrillae which give it the appearance of a halo; companion cells, 1-3, hyaline, smooth, spherical or pyriform, occasionally occurring in tandem; germination unknown.

Parasitic in *Spirogyra* sp., in Belgium (de Wildeman, l.e.) and Germany (Minden, l.e.), causing only slight swelling of the host filaments.

**O. APPENDICULATA** de Wildeman, 1895. I.c., p. 34. 1896. Ann. Soc. Belge Micro. 20: 29. Pl. 1, figs. 4, 8-12. *Pseudolpidiopsis appendiculata* (de Wildeman) Minden, I.c., p. 239.

Zoosporangia solitary, hyaline, smooth, spherical, oval or ellipsoid with a single exit tube which does not project far beyond the surface of the host cell. Zoospores unknown. Resting spores spherical, 13-25  $\mu$ , thick-walled, covered with elongate abruptly tapering, rather well separated spines; companion cell single, hyaline, smooth, vermiform and filamentous, 20  $\mu$  long, and inflated at the end; germination unknown.

Parasitic in *Mesocarpus* sp., in Belgium, causing marked local swellings up to four times the normal diameter of the filaments.

**O. OEDOGONIORUM** Scherffel, 1925. Arch. Protisk. 52: 109. Pl. 4, figs. 199-207c; pl. 5, figs. 207d-208.

*O. fusiformis* var. *Oedogoniarum* Sorokin, 1883. Arch. Bot. Nord. France 2: 29, fig. 31. 1889, Rev. Mycol. 11: 89. Pl. 80, fig. 99.

*Olpidium Oedogoniarum* (?) de Wildeman, 1894. Ann. Soc. Belge Micro. 18: 154. Pl. 6, figs. 9, 10.

Zoosporangia solitary or numerous, up to 5 in a cell, hyaline, smooth, oval, elongate, sac-like, 5-7  $\times$  50  $\mu$ , with one or two short, 3-4  $\mu \times$  4-6  $\mu$ , tapering exit tubes which may project slightly beyond the host cell. Zoospores isocont and diplanetic, hyaline, oval and elongate, 5  $\mu$  long, with a small refringent spot but no conspicuous ventral furrow; flagella lateral, one extending forward and the other backward in swimming; cystospores 3  $\mu$  in diameter. Resting spores hyaline, smooth, spherical, oval, ellipsoid, 10-12  $\mu \times$  14  $\mu$ , thick-walled; content coarsely granular with several small refractive globules surrounding a large central one; resting spore lying free within a hyaline, thin-walled, oval or ellipsoid vesicle (oogonium ?); companion or male cell solitary, hyaline, oval or spherical, 10  $\mu$ , germination unknown.

Parasitic in *Oedogonium* sp., in Hungary (Scherffel, I.c.) and New York, U. S. A. (Sparrow, '33), destroying the content of the algal cell but not causing hypertrophy.

Scherffel believed that *O. fusiformis* var. *Oedogoniarum* Sorokin and *Olpidium Oedogoniarum* de Wildeman are identical to this species. Fischer ('92), however, listed Sorokin's fungus as a synonym of *Olpidium entophytum*, while Minden regarded it as identical to de Wildeman's *O. Oedogoniarum*. Since Sorokin and de Wildeman observed only zoosporangia the questions of identity and synonymy of their species cannot be answered at present, although both species occur in the same host.

The development of the resting spore in a vesicle, which Scherffel and Sparrow interpreted as a true oospore in an oogonium without periplasm, and the manner of zoospore formation and behavior are strikingly similar to those of *Lagenidium Oedogonii* Scherffel, while the thallus and zoosporangia are

like those of *Olpidiopsis*. For these reasons Scherffel was uncertain as to which of the two genera this species belongs and believed that it possibly may be a transition form between *Olpidiopsis* and *Lagenidium*.

#### **O. ANDREEI** (Lagerheim) nov. comb.

*Pleotrichelus andréei* Lagerheim, 1899. Ymer 1: 436.

*P. Ectocarpi* Jokl, 1916. Österr. Bot. Zeitschr. 66: 267. Pls. 4, 5.

*Petersenia (Olpidiopsis) andréei* (Lagerheim) Sparrow, 1936. Biol. Bull. 70: 245. Figs. 1-8, 12.

Zoosporangia solitary or numerous, up to 23 in a cell, spherical, 3-80  $\mu$ , oval, ellipsoid, 8-15  $\mu \times$  15-25  $\mu$ , polygonal or irregular with 1-10 tapering or irregular exit tubes, 3.5-10  $\mu$  in diameter and 6-78  $\mu$  long, which may penetrate adjacent cells and project to the outside beyond the surface of the host, or open within the host cell. Zoospores ellipsoid, somewhat pyriform, arched or curved 3  $\times$  4-5  $\mu$ , with a large refractive spot at the narrow anterior and broad posterior end; occasionally liberated within the host cell. Resting spores, parthenogenetic (?) or sexual, spherical or slightly ellipsoid, 12-23  $\mu$ , brown, smooth and thick-walled; companion or male cell when present single, hyaline, spherical, 5-12  $\mu$ , or slightly oval; germinating by becoming transformed directly into a zoosporangium with an exit tube.

Weakly parasitic and possibly saprophytic in the vegetative cells and plurilocular sporangia of *Spongomyces* sp., in King Charles Land (Lagerheim, I.c.); *Aerosiphonia incurva*, and *Aerosiphonia* sp., in Greenland and Denmark (Petersen, '05; Sparrow, '34); *Ectocarpus granulosus* in the Gulf of Trieste (Jokl, '16), and *E. siliculosus* in Mass., U. S. A. (Sparrow, '36); causing slight hypertrophy of the plurilocular sporangia in *Ectocarpus*, and degeneration of the plastids and remainder of the protoplasm.

Although Sparrow placed this species in *Petersenia*, he nevertheless believed that it should be referred to *Olpidiopsis*. Its zoospores, however, are strikingly like those of *Pontisma*. The male and female thalli which fuse to form the resting spore may be equal in size or quite unequal, so that sexual reproduction in this species may be iso- or heterogamous, according to Sparrow. Occasional resting spores without attached empty male cells may also be found, and they have doubtless developed parthenogenetically without fusion.

Sparrow further regarded *P. Ectocarpi* Jokl as identical to this species, and the present writer is listing it provisionally as a synonym. However, inasmuch as Jokl failed to observe flagellate zoospores and resting spores its identity to *O. andréei* is very doubtful at present. According to his observations, the sporangia may occasionally occur extramatrically and send their exit tubes into the algal cell (fig. 164). He further described and figured the newly-entered zoospores and young thalli as naked and amoeboid with several long tenuous, more or less

radially oriented pseudopods (fig. 162). Jokl believed that the amoeba may often migrate towards the nucleus, as in *O. schenkiana* and *O. Oedogniorum*, and engulf it. Very shortly, however, the amoebae retract their pseudopods, round up, and grown into large thalli. Petersen and Sparrow apparently failed to find extramatrical thalli and the amoeboid stages, and it is quite possible that Jokl's fungus relates to another species.

### PARASITES OF RICCIA AND INSECTS

**O. RICCIAE** du Plessis, 1933. Ann. Bot. 47: 761. Figs. 1-12.

Zoosporangia solitary or up to 12 in a rhizoid, oval, elliptical,  $20-35.7 \mu \times 24-40 \mu$ , opening by an irregular fissure or an exit tube. Zoospores heterocont, hyaline, globose or slightly ovoid,  $2.4-4 \mu$ , swarming in the sporangium before dehiscence, liberated within the host cell or to the outside; flagella anterior,  $8.3 \mu$  and  $17.5 \mu$  long respectively, shorter flagellum directed forward and longer one backward in swimming. Resting spores parthenogenetic (?) or sexual, globose, elliptical, elongate or cylindric, often laterally and terminally depressed,  $12.8-32 \mu \times 14.4-48 \mu$ , hyaline or light brown, with a thick warty exospore; companion or male cell hyaline, smooth and spherical; germination unknown.

Parasitic (?) in rhizoids of *Riccia* sp., South Africa, without causing hypertrophy.

**O. UCRAINICA** Wize, 1904. Bull. Intern. L'Acad. Sci. Cracovie. 1904: 713. Figs. 1a-1g.

Thallus broadly oval,  $35 \mu$  in diameter. Zoosporangia and zoospores unknown. Resting spores apparently formed by the contraction and encystment of the thallus content, and lying loose and free in a vesicular membrane until mature, orange or golden in color, spherical,  $20-30 \mu$ ; contents granular with one large  $15-25 \mu$ , or several small,  $3-5 \mu$ , refringent globules; wall thick, sculptured and reticulate; companion cell lacking.

Parasitic in the larvae and pupa of *Cleonus punctiventris* and *Anisplia austriaca* in Repiszna, Ukraina, and Ruthenia, filling the insects' bodies with an orange-colored granular powder.

There is little, if anything at all, in the life cycle of this organism as described by Wize to justify its inclusion in *Olpidiopsis*. Sparrow ('39) believed that Wize's fungus relates to *Myrophagus ucrainicus* Sparrow, a chytrid which Thaxter had collected in 1927. Peteh ('40) likewise held that his earlier-named *Entomophthora* (*Tarichium*) *reticulata* is identical to Wize's and Sparrow's species.

### PSEUDOLPIDIUM

Fischer, 1892. Rabenh. Kryptfl. I, 4: 33.

(PLATE 13, FIGS. 171-190)

Thallus intramatrical, appearing more or less naked but immiscible with the host protoplasm when

young and becoming enveloped by a sharply-defined wall at maturity. Zoosporangia solitary or numerous in a host cell, smooth, variously-shaped with one to several exit tubes of variable diameter and length which may often extend considerably beyond the surface of the host cell. Zoospores hyaline with one to several refractive bodies; somewhat egg-, bean-, or kidney-shaped, oval, elongate, and pyriform; heterocont or isocont (?), flagella laterally inserted

### PLATE 13

*O. andreei*

Fig. 161. Infection of *Ectocarpus* cell. Sparrow, '36.

Fig. 162. Young amoeboid thallus with pseudopods, approaching host nucleus at right. (*Pleotrichelus Ectocarpi*). Jokl, '16.

Fig. 163. Older vacuolate thallus enveloped by a distinct wall. Sparrow, l.c.

Fig. 164. Abnormal, partially extramatrical thallus. Jokl, l.c.

Fig. 165. Zoosporangium. Sparrow, l.c.

Fig. 166. Free hand interpretative drawing of zoospore, heterocont (?). Sparrow, l.c.

Fig. 167. Plasmogamy. Sparrow, l.c.

Fig. 168. Resting spore with small companion cell. Sparrow, l.c.

Fig. 169. Mature parthenogenetic (?) resting spore. Sparrow, l.c.

### *Pseudolpidium*

Fig. 170. Cyst of *Glenodinium* with two thalli of *P. Glenodiniianum*. Dangeard, '88, '89.

Figs. 171, 172. Zoosporangia of same. Dangeard, l.c.

Fig. 173. Emergence of zoospore to form a mass at the mouth of the exit papilla. *P. Glenodiniianum*, Dangeard, l.c.

Fig. 174. Heterocont zoospores, *P. Glenodiniianum*, Dangeard, l.c.

Fig. 175. Zoosporangia of *P. Sphaeritae* in a smooth resting spore of *Sphaerita eudogena*. Dangeard, l.c.

Figs. 176, 177. Heterocont zoospores with a large refractive globule. *P. Sphaeritae*, Dangeard, l.c.

Fig. 178. Empty sporangium in a spiny cyst. *P. Sphaeritae*, Dangeard, l.c.

Fig. 179. Spiny sporangium or possibly a parthenogenetic resting spore of *Pseudolpidium* sp., from the elementary tract of the boll weevil. Krafka and Miller, '26.

### *P. deformans*

(All figures after Serbinow, '07)

Fig. 180. Infection of hair cell of *Draparnaldia glomerata*.

Fig. 181. Amoebae of *P. deformans* in three hypertrophied cells.

Fig. 182. Amoeba with long pseudopods.

Fig. 183. Division of amoeba.

Fig. 184. Fixed and stained preparation of trimucleate amoeba; zoospores case and infection tube attached to host cell.

Fig. 185. Similar preparation of a host cell with eleven rounded amoebae.

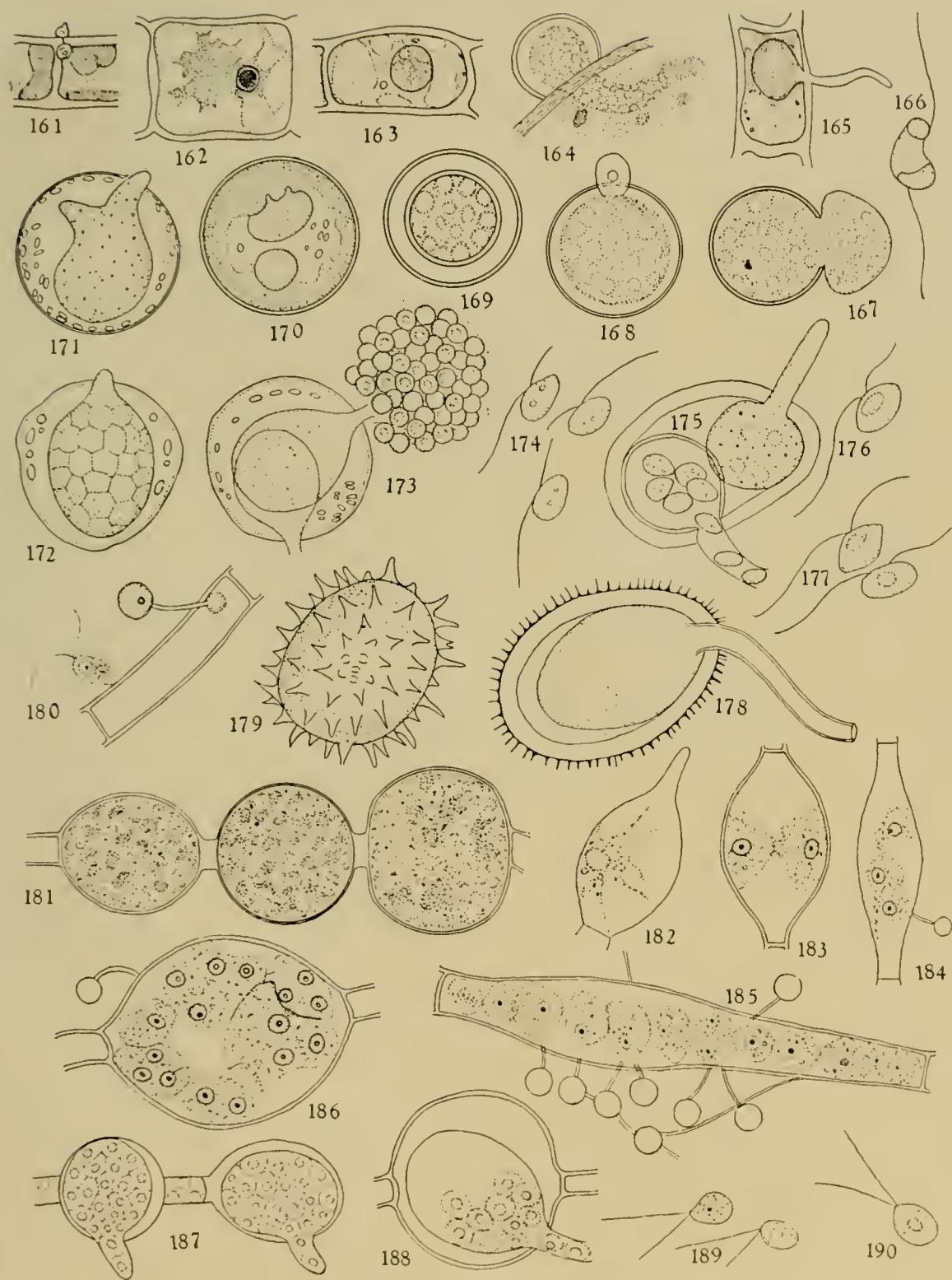
Fig. 186. Hypertrophied cell with six thalli.

Fig. 187. Mature zoosporangia with zoospores.

Fig. 188. Emergence of zoospores.

Figs. 189, 190. Biflagellate zoospores.

## PLATE 13



Olpidiopsis, Pseudolpidium

(?), shorter flagellum extended forward in swimming; emerging singly and fully developed and swimming directly away, or lying quiescent in a globular mass for a few moments at the mouth of the exit tube. Resting spores unknown.

The history of this genus has been discussed in relation to *Olpidiopsis* and need not be repeated here. As noted previously it is retained only as a temporary expedient for three species with biflagellate zoospores in which no resting spores have yet been reported. It is not improbable as McLarty and Shanor have suggested that two of the species will eventually be included in *Olpidiopsis*, while the third one may possibly prove to be related to *Rozellopsis* or *Woronina*.

Zoospore germinating and infection of the host have been described only for *P. deformans*, so that an account of the early developmental stages must be based on this species. As is shown in figure 180 the zoospores come to rest on the host, round up, encyst, and later develop conspicuous germ tubes (figs. 185, 186) which penetrate the host wall. As in *Olpidiopsis* the content of the spore passes through this tube into the host as a naked body, and in all species except *P. deformans* gives rise to one thallus or sporangium. At first the young parasite is more or less indistinguishable from the host protoplasm, but as the latter is killed and partly consumed the parasite may be readily recognized as a small dense mass in the hypertrophied cells (fig. 181).

In *P. deformans* the thallus becomes amoeboid shortly after entering the host cell (fig. 24). It develops numerous long, fine (fig. 182) or blunt pseudopods (fig. 184) and creeps around in the infected cell. After its nucleus has divided it constricts and divides as is shown in figure 183. Serbinow's figures further suggest that the large multinucleate amoeboid thalli also may divide, so that numerous thalli result from a single infection. Whether or not several meronts are formed by a process of schizogony as in the Plasmodiophorales is not certain. Multiple infection, however, is not uncommon (figs. 185, 186), so that the presence of several thalli in one cell does not mean that they have arisen from a single infection. The occurrence of single sporangia in a host cell (figs. 187, 188) suggests that the amoeboid thallus does not always divide and that a zoospore may sometimes give rise directly to one sporangium. The early developmental stages of *P. deformans* are nonetheless suggestive of those of the septigeneous species of *Rozellopsis*, provided the reports that the thallus of this genus undergoes division are true. Minden was accordingly of the opinion that Serbinow's fungus is closely related to genera which develop sporangiosori. Unlike *Woronina polycystis* and species of *Rozellopsis*, the thallus of *P. deformans* is usually distinguishable from the host protoplasm, and no cross walls separate the respective segments of the thallus as in *R. septigena* and *R. simulans*. It differs further from other species of *Pseudopodium* by the lack of oily or fatty

refrangent material in the developing thalli and sporangia, according to Serbinow.

**P. GLENODINIANUM** (Dangeard) Fischer, 1892.  
Rabenh. Kryptfl. I, 4: 36.

*Olpidium Glenodinianum* Dangeard, 1882. Jour. de Bot. 2: 130. Pl. 5, figs. 6-10.

Zoosporangia solitary or up to 4 in a cell, spherical or ellipsoid, size unknown; hyaline and smooth with a short papillae or exit tube which extends slightly beyond the surface of the host. Zoospores emerging fully formed and remaining quiescent for a few minutes in a globular mass at the mouth of the exit orifice before swimming away; spherical at first, later becoming oval or ellipsoid, size unknown; flagella laterally inserted, shorter flagellum extending forward and longer one projecting backward in swimming. Resting spores unknown.

Parasitic in *Glenodinium cinctum* in France, completely killing and destroying flourishing cultures.

According to Dangeard this species had been frequently observed before his time, but its thallus and zoospores were mistaken for germination stages of the hosts as well as those of *Ceratium fuscus* and *C. tripos*.

**P. SPHAERITAE** (Dang.) Fischer, l.c., p. 36.

*Olpidium Sphaeritae* Dangeard, 1889. Le Bot. 1:51. Pl. 3, figs. 3-7.

*Olpidiopsis Sphaeritae* (Dang.) Schroeter, 1897. Engler und Prantl, Nat. Pflanzf. I, 1: 69.

Zoosporangia solitary or up to 6 in one host cell, hyaline, smooth, spherical, or ellipsoid, size unknown, with a single exit canal which projects far beyond the surface of the host cell. Zoospores small, size unknown, hyaline with one to several refractive granules; flagella laterally (?) inserted, shorter one extending forward in swimming. Resting spores unknown.

Parasitic in the resting spores of *Sphaerita endogena* in France.

This species has not been reported since 1889 and nothing further is known about its life history and structure besides the original description of Dangeard.

**P. DEFORMANS** Serbinow, 1907. Scripta Bot. Hort.

Imp. Univ. Petrop. 24: 25, 154. Pl. 1, figs. 1-12; pl. 4, figs. 16-28.

Thallus more or less naked, amoeboid, constricting and dividing to form additional thalli. Zoosporangia solitary or up to 11 in a host cell, hyaline, smooth, spherical,  $35 \mu$ , or elongate and ellipsoid,  $14.7-27 \mu \times 47.5 \mu$  with a broad elongate,  $8 \times 15.8 \mu$ , exit tube which projects considerably beyond the surface of the host cell. Zoospores, hyaline, spherical or oval,  $3.15-4.75 \mu$ , often changing shape; flagella laterally inserted; emerging singly, fully developed and swimming directly away. Resting spores unknown.

Parasitic in *Draparnaldia glomerata* in Russia, causing marked hypertrophy of the host cells.

The above description is taken from a German résumé of the Russian text. Because the thallus of *P. deformans* is amoeboid and undergoes division into secondary thalli, Serbinow was uncertain about the taxonomic position of this species, and he accordingly assigned it only temporarily to *Pseudolpidium*.

Another questionable and unidentified species of *Pseudolpidium* was found by Krafka and Miller ('26) in the alimentary tract of the boll weevil in Georgia. These workers did not study its life cycle and merely reported and figured a few spiny, oval,  $10-44 \mu \times 42-50 \mu$ , resting spores or sporangia (?). Whether these bodies are parthenogenetic resting spores or spiny zoosporangia of *Pseudolpidium* or relate to an entirely different organism is not evident from Krafka and Miller's description.

Whether or not the parasite which Nägler ('11) found in *Euglena sanguinea* and described as *Pseudosphaerita Euglenae* belongs here is questionable. The presence of long exit tubes seems to exclude it from *Pseudosphaerita* so far as this genus is now known, and the zoosporangia are suggestive of those of *Olpidiopsis* and *Pseudolpidium*. However, until the zoospores have been observed the identity of Nägler's fungus will remain doubtful.

## PSEUDOSPHAERITA

Dangeard, 1895. Le Bot. 4: 243.

(PLATE 14)

Thalli intramatrical, solitary or up to 25 in a cell, appearing to be more or less naked but immiscible with the host protoplasm when young; becoming invested with a definite wall or membrane as they mature; oval, spherical, coiled, elongate, or slightly irregular. Zoosporangia of same shape and size as the mature thalli; exit papillae apparently lacking; opening by a rupture (?) of the wall. Zoospores heterocont or isocont (?) with flagella inserted near the anterior end, short flagellum directed forward in swimming while the longer one is dragged along behind; liberated to the outside (?) or inside the host cell where they may start secondary infections. Resting spore unknown.

This genus resembles *Sphaerita* superficially but according to Dangeard's latest study ('33) differs fundamentally from the latter genus by the division or segmentation of its thallus after each successive mitosis (figs. 9-15), with the result that multinucleate thalli are rarely formed. The segments become progressively smaller with each division and are eventually transformed directly into zoospores (fig. 17). Dangeard, nevertheless, figured multinucleate thalli both in 1895 (fig. 3) and 1933 (fig. 8), which suggested to him that he may have had two organisms at hand or that *Pseudosphaerita* has two extreme types of development with intermediate

stages between. In his latter contribution, Dangeard held to the former possibility, while Mitchell ('28) upheld the second viewpoint. The latter worker reported that the parasite which he found in *Euglena caudata* segments after each nuclear division (figs. 19-22), while the one occurring in *E. viridis* develops a multinucleate thallus and finally undergoes cleavage into spore rudiments (figs. 23-27). According to his account these are but different stages of the same parasite. However, the identity of Mitchell's species is uncertain because he did not observe the zoospores nor the number, relative lengths and position of the flagella. The similarity in types of development nonetheless suggests that his species are the same organisms studied by Dangeard in 1895 and 1933, and for this reason they are included in Plate 14. Jahn ('33) maintained that the species with the multinucleate "plasmoidal" stage (figs. 23-27) is *Sphaerita dangeardii* Chatton and Brodsky, 1909. Obviously, more intensive study of both *Sphaerita* and *Pseudosphaerita* is necessary before the latter genus can be adequately diagnosed and discussed in relation to other genera with biflagellate zoospores.

Dangeard and Mitchell did not observe infection of the host, so that it is not known whether the zoospores enter the *Euglena* cell directly or germinate on its surface and then leave the empty spore case and penetration tube behind as in *Olpidiopsis*, *Eurychasma*, etc. In instances where the zoospores are discharged within the host cell (fig. 18) they apparently develop directly into thalli (6-8). As noted above, Dangeard figured several multinucleate thalli which appear to be undergoing cleavage (figs. 4, 5), but this appearance is due to the complete or partial disappearance of the lines of demarcation of the zoospores in the late stages of development, according to Dangeard's latest account. As a result the mature thallus may appear to be homogeneous and multinucleate (figs. 3, 16) or divided into large irregular multinuclear segments (figs. 4, 51). The type of cytokinesis suggested by the latter two figures appears to be quite different from that illustrated in figures 10 to 14 and 19 to 22. Here the whole thallus appears to be partitioned or fragmented after each mitosis, while in figures 4, 5, and 27 it looks as if the content of a sporangium has undergone endogenous division with the original thallus wall remaining intact.

The method by which the zoospores get out of the host is not known. According to Dangeard they are liberated within the host, but it is obvious that some of them eventually escape. Otherwise additional hosts would not become infected. Mitchell suggested that they might escape through the "mouth" vacuole or by rupture of the host cell. The mature free swimming zoospores are pyriform and pointed at the apex with two unequal flagella inserted a short distance back of the anterior end (fig. 1). Their movement in swimming is more even, straight forward and less irregular and darting than in *Sphaerita*.

According to Dangeard, the structure and activity of *Euglena polymorpha* are not greatly affected at first by the presence of the parasite, and in exceptional cases of monoinfection this host may continue its normal activities even after the parasite is mature. The plastids may remain green and unchanged, except for a reduction in size, up to the time of sporulation (figs. 16, 17). In instances of heavy infection, however, the injurious effects may appear sooner. As the parasites develop and mature the starch grains become corroded, the chloroplasts turn lighter in color, and the cytoplasm becomes reduced in quantity. The vacuome, stigma, and nucleus, on the other hand, remain normal for a longer time. The initial effect on the nucleus is an increase in chromaticity as densely stainable rods and fragments appear in the reticulum. Later the nucleus decreases in size and finally disintegrates. Like the remainder of the host cell it does not enlarge or divide because of the presence of the parasite. Mitchell also reported that the parasite has no toxic effect on *E. caudata*. No differences in activity could be detected in infected individuals, although some of them were so crowded with parasites that little or no green color was visible. In *E. viridis*, on the other hand, infected specimens were nearly always rounded, and in fixed and stained preparations early degeneration of the nucleus and chromatophores was evident in such individuals. In the late stages of development the parasite was often enveloped by a mass of degenerating cytoplasm, including traces of the host nucleus and plastids.

*Pseudosphaerita* includes at present *P. Euglenae* and possibly another species, *P. radiata* comb. nov. However, the reports of Pumaly ('27) and Cejp ('35) that *Sphaerita endogena* and *S. dangeardii* have biflagellate zoospores suggest that additional species exist. It is equally possible that *Sphaerita* may have biflagellate zoospores and does not differ fundamentally from *Pseudosphaerita*. The parasite of *E. sanguinea* described by Nägler ('11) as *P. Euglenae* probably does not relate to this species because it develops long exit tubes like *Pseudolpidium Sphaeritae*. The taxonomic position of *Pseudosphaerita* and its relation to other genera with biflagellate zoospores is very uncertain at present. Dangeard ('95) first regarded it as a member of simple olpidiaceous chytrids closely related to *Sphaerita*, but in 1933 he created a separate family, *Pseudosphaeritaceae*, for it among the Archimycetes because of its characteristic type of development. Mitchell included the species which he studied in the Sporozoa under the Haplosporidia.

#### P. EUGLENAE Dangeard, 1895. l.c., fig. 9. 1933, ibid. 25; 36. Pl. 4, figs. 3-16.

Zoosporangia solitary or numerous, oval, spherical, elongate, coiled, or slightly irregular, hyaline and smooth, forming 64 to 128 zoospores. Zoospores pyriform,  $2.5-3 \mu \times 6 \mu$ ; flagella 2.5 and 7  $\mu$  long respectively. For further details see the generic description above.

Parasite in *Euglena viridis* and *E. polymorpha* in France (Dangeard, l.c.); *E. caudata* in Georgia, U. S. A. (Mitchell, l.e.).

This species is possibly the parasite with pyriform biflagellate zoospores which Stein (1878, Abt. III, 1, Pl. 20, fig. 21) figured in *E. viridis* in Germany. He also illustrated parasites with biflagellate zoospores in *Chlamydomonas alborviridis* (Pl. 14, figs. VI 4-14) and *C. pulvisculus* (Pl. 15, fig. 36), but since the flagella are posteriorly attached it is doubtful that these parasites relate to *Pseudosphaerita*.

#### P. RADIATA (Dangeard) comb. nov.

*Sphaerita radiata* Dangeard, 1890. Le Bot. 2: 54. Pl. 2, fig. 20.

Zoosporangia solitary or up to 3 in a cell, hyaline, smooth, oval and egg-shaped, size unknown; liberated or expelled to the outside by the rupture of the host cell. Zoospores hyaline with a refractive globule, oval and elongate, isocont (?), size unknown; liberated by the breakdown of the sporangium wall. Resting spore unknown.

#### PLATE 14

(Figs. 2-5 after Dangeard, '95; figs. 1, 6-8 after Dangeard, '33; figs. 28-31 after Dangeard, '90; figs. 19-27 after Mitchell, '28.)

#### *Pseudosphaerita Euglenae*

Fig. 1. Biflagellate heterocont zoospores with flagella inserted in a small depression near the anterior end; shorter flagellum directed forward.

Fig. 2. Uninucleate oval parasite (*Sphaerita* sp. ?) in *E. viridis*.

Fig. 3. Multinucleate coiled thallus.

Fig. 4. Cleavage stages (?) of multinucleate thalli.

Fig. 5. *Euglena polymorpha* with 17 uninucleate parasites which have apparently developed from zoospores liberated within the host cell.

Fig. 6. Uninucleate parasites slightly larger.

Figs. 7, 8. Uni- and multinucleate parasites.

Figs. 9-15. Stages in the division of the parasites following each mitosis.

Fig. 16. A multinucleate parasite shortly before sporogenesis.

Fig. 17. Sporangium with fusiform zoospores.

Fig. 18. Zoospores liberated within host cell.

Fig. 19. *Euglena caudata* with one uninucleate thallus.

Figs. 20-22. Successive stages of growth and division of the thallus into spores in *E. caudata*.

Fig. 23. Two uninucleate thalli (*Sphaerita dangeardii* ?) in *E. viridis*.

Fig. 24-26. Stages in the development of a multinucleate thallus in *E. viridis*.

Fig. 27. Sporangium filled with spherical and oval spores.

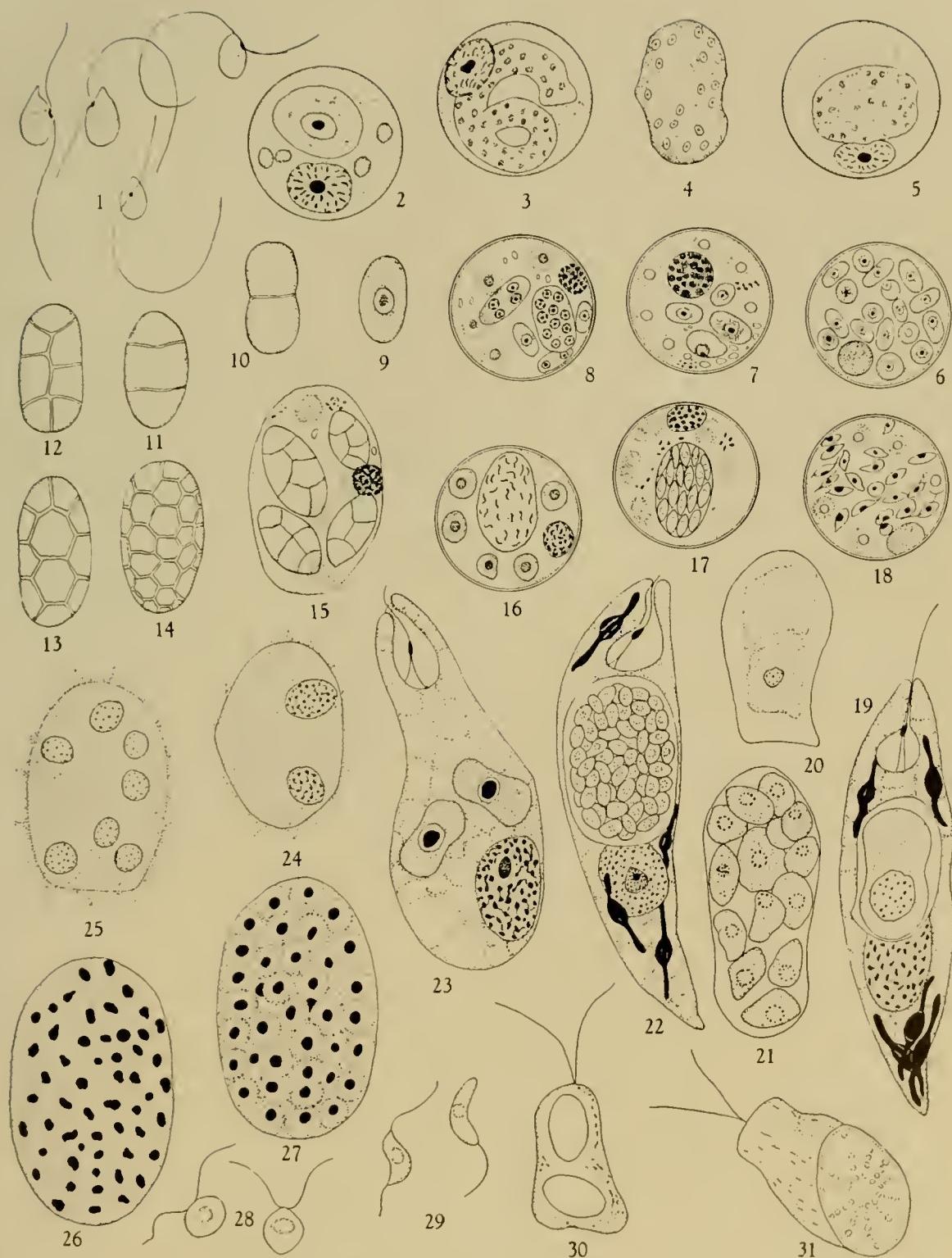
#### *Pseudosphaerita* (?) *radiata*

Figs. 28, 29. Biflagellate iso- and heterocont and uninflagellate zoospores.

Fig. 30. *Cryptomonas ovata* with two small parasites.

Fig. 31. *Cryptomonas ovata* with a large parasite in which the refractive globules are radially oriented.

## PLATE 14



Parasitic in *Cryptomonas ovata* in France.

This species was apparently observed by Dangeard in 1889 (Pl. 1, fig. 15) and mistaken for the endogenous germs of the host. Its outstanding characteristic, according to Dangeard ('90), is the radial orientation of the refractive globules in the thallus (fig. 31). The inclusion of this species in *Pseudosphaerita* is obviously questionable, because the thallus is expelled from the host as in species of *Sphaerita*. Although Dangeard figured most of the zoospores as biflagellate he failed to include this species in *Pseudosphaerita*. Nevertheless, it is included here tentatively although nothing is known about the development of the thallus and the type of cytokinesis.

The oval and elongate "nuclei" which Stein (1878, pl. 19, figs. 29, 31) figured in the same host may possibly relate to this species, although no radially oriented refractive globules are shown.

## BLASTULIDIOPSIS

Sigot, 1931. C. R. Soc. Biol. 108: 37.

(PLATE 17, FIGS. 10-12)

Thallus intramatrical, unicellular, lobed, plurilocular, irregular, and holocarpic. Zoosporangia solitary in host cell, hyaline, smooth, irregular, lobed and plurilocular with a low exit papilla. Zoospores biflagellate and isocont, developing completely and swarming in the zoosporangium, swimming directly away after emerging. Resting spores unknown.

The thallus of this monotypic genus is very similar in appearance to that of *Blastulidium*, but the type of infection and thallus development are more like those of species of the family *Lagenidiaceae*. The zoospore comes to rest on the *Cyclops* egg and forms a germ tube which penetrates the host wall. The content of the spore does not pass into the host cell as a more or less naked protoplast as in *Olpidiopsis*, *Ectrogella*, etc., but instead the tip of the penetration tube enlarges, elongates, branches and eventually forms the irregular lobed thallus. Sigot did not observe germination, infection and the stages of thallus development in living material, but based his account on studies of fixed and stained preparations. In the early stages of development, the thallus contains numerous small vacuoles (fig. 10) which later fuse to form a large central one. By this time the contents of the host cell have been largely consumed, and the parasite usually occupies the entire cavity. After the vacuoles have fused, the more viscid, visible part of the protoplasm forms a thin parietal layer in which the nuclei lie (fig. 11). Cytokinesis is apparently accomplished by centrifugal cleavage furrows which cut out uninucleate spore rudiments. The latter develop into zoospores which soon begin to swarm within the sporangium. Shortly thereafter the tip of the exit papilla deliquesces, and the zoospores swim out and away. No evidence of

diplanetism has so far been observed. As is shown in figure 12, the zoospores are oval and slightly elongate with two flagella inserted near the anterior end at which lies a conspicuous refractive globule, similar to that described by Sparrow ('34, '36) for the zoospores of *Siroplidium* and *Petersenia*.

The taxonomic position and relationships of *Blastulidiopsis* are obscure, since nothing is known about its resting spores. As noted previously its type of development, according to Sigot, is suggestive of species of the *Lagenidiaceae*, while the appearance of the centrally vacuolate sporangia, swarming of the zoospores within, etc., are similar to those of *Olpidiopsis*, *Siroplidium*, *Petersenia* and other related genera.

**B. CHATTONI** Sigot, l.c., figs. 1-3.

Zoosporangia solitary, hyaline, smooth, irregular and lobed, size unknown. Zoospores  $6 \times 8 \mu$  with a refractive globule at the anterior end; flagella 15-20  $\mu$  long, inserted near the anterior end and extending in opposite directions. Resting spores unknown.

Parasitic in eggs of *Cyclops* in France, destroying their content but causing no enlargement or division of the inflated cell.

## PYTHIELLA

Couch, 1935. Mycologia 27: 160.

(PLATE 15)

Thallus intramatrical, holocarpic, oval, ellipsoid and spherical; solitary or up to 4 in a swelling. Zoosporangia centrally vacuolate with 1 to 5 simple or branched exit tubes. Zoospores fully delimited in the zoosporangia, diplanetic; primary zoospores biflagellate, gliding out and encysting at the tip of the exit tube; content of cysts emerging after about an hour; motile secondary zoospores oblong with a longitudi-

### PLATE 15

#### *Pythiella vernalis*

Fig. 1. Germinated zoospore with young parasite within *Pythium* hypha.

Fig. 2. Beginning of host hypertrophy.

Figs. 3-7, 9-13. Successive stages of the maturation of a thallus into a zoosporangium, cleavage, zoospore emission, encystment, and emergence from cysts.

Fig. 8. The so-called escauloped or "balled" stage of sporogenesis.

Fig. 9. The homogeneous stage following cleavage.

Figs. 14-16. Successive stages of emergence of the zoospore from a cyst.

Fig. 17. A mature biflagellate isocont zoospore.

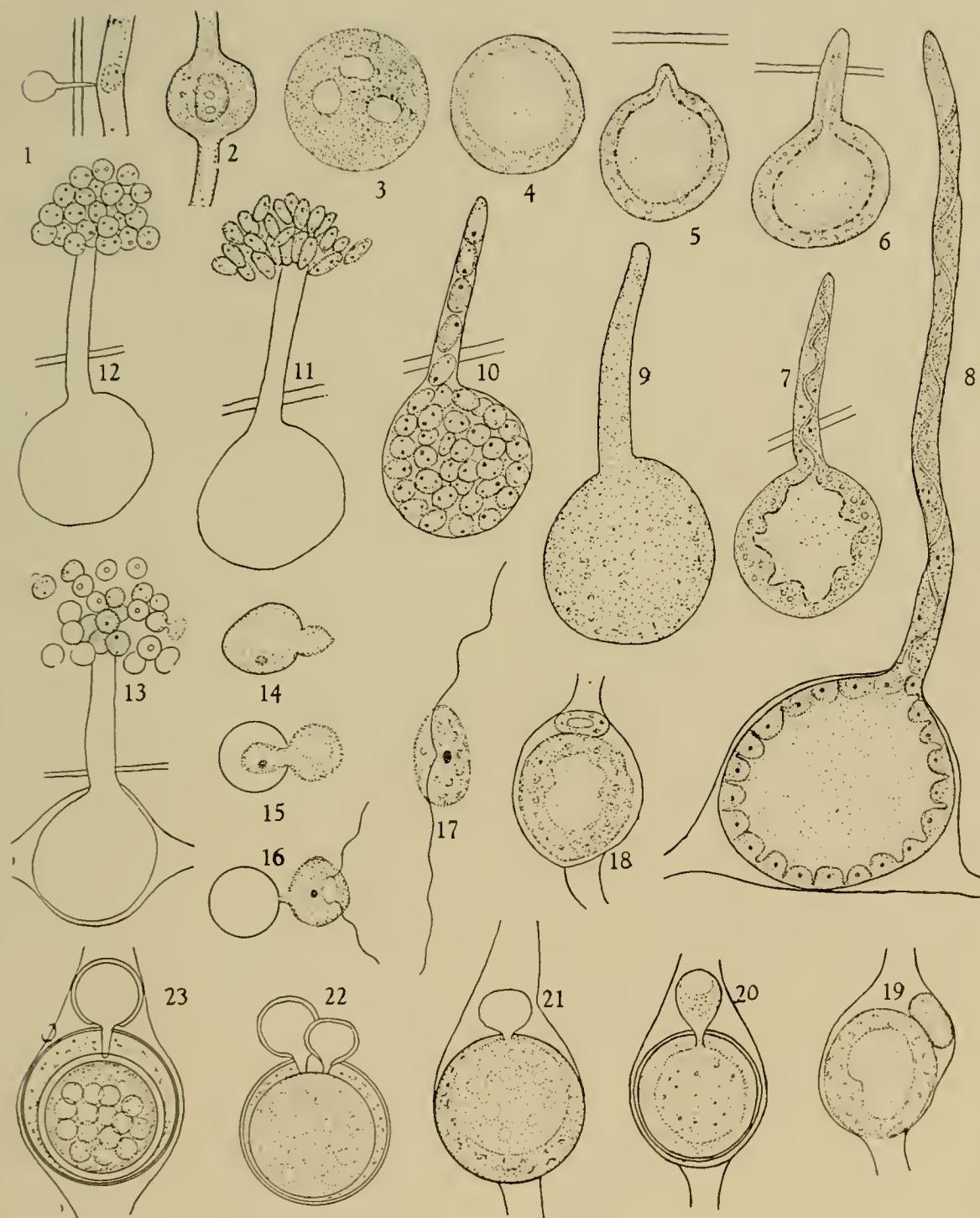
Figs. 18, 19. Young antheridia and oogonia in hyphal swellings.

Figs. 20, 21. Beginning and completion of plasmogamy.

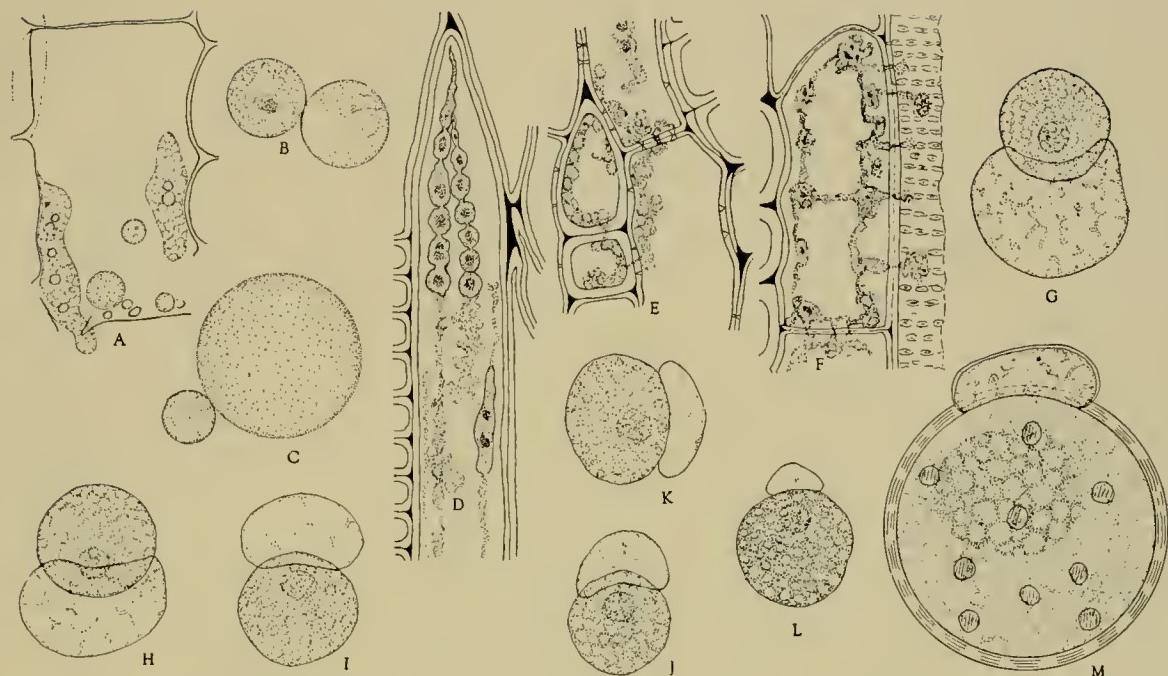
Fig. 22. An egg fertilized by two antheridia.

Fig. 23. Mature oospore within an oogonium and an empty attached antheridium.

## PLATE 15



Pythiella



*Carpenterella* sp. (?)

Text-fig. A. Amoeboid thalli and spherical bodies in sugar cane. Drawn from photograph 5B after Carpenter, '40.

Text-fig. B. Two almost equal, paired spherical bodies. Drawn from photograph 7, left, after Carpenter, '40.

Text-fig. C. Association of a large and a small sphere. Drawn from photograph 7, right, after Carpenter, '40.

*Carpenterella Molinea*  
(All figures after Tehon and Harris)

Text-fig. D. "Thalli in fiber cell showing plasmoidal enlargements and bead-like knots."

Text-fig. E. "Thallus in ray and wood parenchyma cells, showing connections through pits."

Text-fig. F. "Net-like thallus in parenchyma cell, sending plasmic projections into an adjoining trachea through half bordered pits."

Text-figs. G to L. "Stages in the formation of the oospore, showing shrinkage of the male cell to form the companion cell of the oospore."

Text-fig. M. "Mature oospore with dense alveolar cytoplasm, granules, heavy wall, and companion cell."

dinal groove, laterally biflagellate and isocont, one flagellum directed forward, the other backward in swimming; swimming movement slow in a spiral path, zoospores rotating on their axes. Oospores formed by the fusion of the contents of one or more small thalli (antheridia ?) and an egg cell (?) lying within a rudimentary (?) oogonium; fusion canal fine and delicate; male thalli remaining attached to the oogonium as empty hyaline vesicles or companion cells; germination unknown.

This genus includes a single species, *P. vernalis*, which combines in its life cycle many of the characters of the *Olpidiopsidaceae*, *Lagenidiaceae*,

*Saprolegniaceae*, and *Pythiaceae*. It is strikingly similar to *Ectrogella*, *Aphanomyopsis*, *Achlya* and *Saprolegnia* in the method of formation and behavior of the zoospores, but differs from these genera, according to Couch, by the appearance of its protoplasm which has a pale whitish fatty gleam like that of *Lagenidium*, *Myzocytium*, *Olpidiopsis*, etc. In type of sexual reproduction it resembles to some degree *Olpidiopsis schenkiana*, but differs from this species by the presence of periplasm in the oogonium. By the latter character it resembles species of *Pythium*.

*Pythiella vernalis* parasitized *Pythium gracile* and *P. dictyosporum* which in turn are parasitic in species of *Spirogyra*. As is shown in figure 1 the zoospore of *P. vernalis* comes to rest on the *Spirogyra* filament, encysts, and then develops a fairly long germ tube which penetrates the algal cell until it reaches the *Pythium* hyphae within. The latter is then pierced, and the content of the zoospores passes into the host cell as a more or less naked globule of protoplasm (fig. 1), like that of *Olpidiopsis*, *Ectrogella*, etc. The zoospore case and penetration tube remain behind and persist for a long time after infection. The young parasite assumes a spherical or oval shape in the *Pythium* hyphae (fig. 2), but it is not certain that it possesses a well-defined wall in the early stages of development. Couch believed that it may be enveloped by a membrane at this stage, but his figures do not show it. No evidence of amoeboid movement or migration of the young parasite has been observed. As the thallus develops, the host hyphae enlarge in the region of infection so that broadly oval, spindle-shaped and spherical swellings or galls are produced (figs. 2, 13, 18-23). However, the host does not form cross septa and delimit

the parasite as in cases of infection by species of *Rozella*. The young thallus usually includes a large number of small vacuoles (fig. 3), and as it becomes larger these increase in size also and eventually fuse to form a large central vacuole (fig. 4). As in the sporangia of *Saprolegnia* species, this vacuole may extend up through the center of the exit tube and often follows a spiral path (figs. 7, 8). The wall of the thallus and sporangia is well defined at maturity, but, unlike that of *Olpidiopsis* and other similar fungi, does not show a marked cellulose reaction when tested with chloro-iodide of zinc. The exit tubes may be simple or branched and vary from 1 to 5 per sporangium. They are usually quite long and extend not only beyond the host cell but through the wall of the *Spirogyra* filament and far beyond its surface.

The central vacuole increases in size as the sporangia mature until the remainder of the protoplasm forms a comparatively thin parietal layer (figs. 4-8). The border of the vacuole becomes quite irregular as broad cleavage furrows are formed (fig. 7) which progress centrifugally towards the periphery. Just before these furrows reach the plasma membrane the parietal layer of protoplasm has a characteristic scalloped appearance (fig. 8) which corresponds to the so-called spore initial stage in the Saprolegniaceae and the "balling" stage described by Scherffel ('25) for *Ectrogella* and *Aphanomylopsis*. As the cleavage furrows attain the periphery the central vacuole collapses and disappears. The boundaries of the cleavage segments become quite invisible and the protoplasm appears to occupy the entire volume of the sporangium (fig. 9). The latter decreases slightly in size at this stage, due possibly to loss of water during the collapse of the central vacuole. This stage is strikingly similar to the so-called homogenous phase of sporogenesis in *Olpidiopsis*, *Ectrogella*, and the Saprolegniaceae. Very shortly afterwards the fully formed spores become visible (fig. 10) and soon glide out of the sporangium as the tip of the exit tube ruptures (fig. 11). They are first elliptical in shape and contain two or more conspicuous granules, but soon round up and encyst and thus form a cluster around the tip of the exit canal (fig. 12) as in *Achlya* and species of *Lagenidium*, *Ectrogella*, *Aphanomylopsis*, etc. Within an hour or two the content of the cyst emerges (figs. 13-16) and is transformed into an oblong biflagellate isocont zoospore (fig. 17) which soon swims away.

Sexual reproduction in *P. vernalis* is heterogamous. The so-called antheridium and oogonium are quite unequal in size and lie in the same gall or swelling (fig. 18). The antheridium shows no structural differentiation as a gametangium, and it is accordingly questionable whether or not it should be designated as an antheridium in the original sense of the term. The oogonium, on the other hand, contains a large central vacuole and parietal layer of protoplasm which appear to undergo some degree of differentiation into ooplasm and periplasm, according

to Couch's description. The antheridium forms a fine fusion canal which penetrates the wall of the oogonium into the ooplasm (figs. 20, 21). The content of the antheridium thereby flows into the ooplasm and fuses with it. As the zygote matures it forms a fairly thick wall, while most if not all of the periplasm gradually disappears (fig. 23). Occasionally two antheridia may fertilize one egg cell (fig. 22) as in species of *Olpidiopsis*.

Nothing is known concerning the origin of the respective gametes in this genus. Whether the thalli which develop into the antheridium and oogonium respectively are derived from zoospores from the same or different zoosporangia is not known. It is accordingly impossible to say at present whether sex differentiation is genotypic or phenotypic. Furthermore, it remains to be seen whether the gametes are multinucleate and their nuclei fuse in pairs or all but one nucleus in each gamete degenerate before karyogamy occurs.

#### P. VERNALIS Couch, I.c., figs. 1-27.

Zoosporangia solitary or up to 4 in a swelling, spherical or subspherical, 10-30  $\mu$ , sometimes flattened when several occur in a gall; exit tubes up to 50  $\mu$  long by 4  $\mu$  in diameter. Motile zoospores 3.7-4  $\mu$  in diameter. Oogonia spherical or subspherical, 11-18.5  $\mu$ . Antheridia hyaline, smooth, slightly flattened or spherical, 5  $\mu$ . Oospore spherical, 9-15  $\mu$ , hyaline, smooth and thick-walled.

Parasitic in *Pythium gracile* and *P. dictyosporum* in North Carolina, U. S. A.

In connection with the Olpidiopsidaceae brief mention may be made of two unusual and incompletely known parasites which Carpenter ('10), and Tehon and Harris ('41) described as forming oospores in somewhat the same manner as *Olpidiopsis*. However, in referring to them here the author does not imply that they should be included in the Olpidiopsidaceae as this family is now recognized, because their thalli are amoeboid and plasmodium-like, and zoospore are not definitely known to occur. The first of these fungi was reported by Carpenter to be associated with chlorotic streak disease of sugar cane in Hawaii. Two developmental phases of the parasite were observed, but the connection between them was not definitely established by Carpenter. The first phase consists of a naked amoeboid or plasmodium-like thallus (text-fig. A) suggestive of that of the Plasmodiophorales and Woroninaceae. However, no individual movement of the thallus or streaming of the protoplasm was observed, nor does the parasite cause cell stimulation or hypertrophy of the host tissues. The second and most conspicuous phase consists of spheres of protoplasm which occur in the parenchyma of the stalk and vary from 5-60  $\mu$  in diameter and hyaline to gray, brown or black and opaque in color. The hyaline spheres, 3-25  $\mu$ , may have thick walls and resemble hypnospores which, according to Carpenter, "appear to be formed by copulation of two units, the content of one sphere

entering the other to form hypnospores, while the empty sphere may remain as a companion cell." (Text-figs. B, C.) Carpenter was uncertain of the identity and relationships of his fungus. Nonetheless, he referred to it as a chytrid and frequently compared it with *Physoderma maydis*.

The second of these fungi was reported by Tehon and Harris as inhabiting the xylem of a diseased Moline elm from Wisconsin. It is very similar to the species found by Carpenter, and they accordingly named it *Carpenterella Molinea*. Its vegetative thallus may appear in two slightly different forms, one elongate, attenuate and thread-like with few to many enlargements (text-fig. D), the other amorphous and amoebic in appearance (text-fig. E). This vegetative phase occurs in wood parenchyma, wood fiber, and ray cells but not in tracheae. The thallus may be confined to one cell or extend through pits in the walls to adjoining cells (text-fig. F). The thalli figured by Tehon and Harris are somewhat suggestive of the pseudo-plasmodium of *Labyrinthula*, but the bead-like enlargements are not as distinctively spindle-shaped and cellular as those of the latter genus. No zoosporangia have been found in *C. Molinea*, but the occurrence of zoospores is suggested "by the presence in some host tracheae of numbers of minute, mononucleate, rounded plasmodium-like bodies, some few of which seem to possess a single polar cilium," according to Tehon and Harris. They have not, however, observed motile flagellate cells.

The origin of the so-called male and female thalli which are reported to fuse is not clear and certain, but Tehon and Harris believed that the swollen ends of strands of the thallus which project into the tracheae (text-fig. F) become detached and assume a spherical shape. These spheres later become associated in pairs, and as the staining reaction of one of them increases in intensity the other sphere becomes more hyaline and empty and decreases in size (text-figs. G-L). This shrinkage was interpreted by Tehon and Harris to mean that the protoplasm of one sphere had flowed into the other, and they accordingly designated the two thalli as male and female. They reported that the fusing thalli are equal in size, but text-fig. G shows clearly that the male cell may be considerably larger than the female. The mature resting spore or oospore is spherical, 10  $\mu$ , with dense opaque protoplasm and numerous refractive globules, smooth, thick-walled, and accompanied by a small hemispherical or lunate companion cell (text-fig. M). Germination of these spores has not been observed.

Tehon and Harris regarded their fungus as a chytrid but were not certain about its taxonomic position. They believed that the character of the thallus and the presence of a vesicle or companion cell on the resting spore indicate relationships with the Woroninaceae (interpreted in the sense of Minde) or the Olpidiaceae. They accordingly placed *C. Molinea* and Carpenter's fungus in the latter

family near *Pseudolpidiopsis*. This disposition is obviously untenable because *Pseudolpidiopsis* is synonymous with *Olpidiopsis* and belongs in the Olpidiopsidaceae. Whether or not these fungi belong in the last named family will not be certain until the presence or absence of zoosporangia and zoospores has been demonstrated. The method of resting spore formation is nevertheless very similar to that of many species of the Olpidiopsidaceae, while the amoebic, plasmodium-like vegetative thallus suggests some relationship to or a parallelism in development with the Plasmodiophorales and the family Woroninaceae as these groups have been interpreted by the author. While the origin and phylogeny and relationships of *Carpenterella* are not clear, it is nevertheless a significant genus and serves to emphasize again that there may be many more simple fungi to be found, the discovery of which will doubtless change many of our present-day concepts concerning the Phycomycetes.

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## Chapter V

### Sirolpidiaceae

Sparrow, 1942. Mycologia 34: 113.

THIS FAMILY was established by Sparrow for the genera *Sirolpodium* and *Pontisma* which Petersen ('05) had previously made the basis of the family Holochytriaceae. Thirteen years earlier, however, Fischer ('92) had proposed the same family name as an alternate for the Aneylistaceae to include *Myzocytium*, *Achlyogeton*, *Lagenidium* and *Ancylistes*. There was thus no agreement between Petersen and Fischer as to which genera comprise the Holochytriaceae, but they nevertheless placed it in the Mycophytridiales. While the Holochytriaceae may have priority over Sparrow's family name, the suffix *chytriaceae* carries the connotation that these fungi are chytrids, which is incorrect in light of present-day knowledge. The name is therefore no longer appropriate and descriptive. The present author is accordingly adopting the Sirolpidiaceae in preference to the Holochytriaceae, but only as a temporary convenience because it is not at all certain that *Sirolpodium* and *Pontisma* constitute a distinct family. So far only vegetative thalli, zoosporangia, and zoospores have been adequately described, and very little, if anything, conclusive is known about the resting spores and their method of development.

Since the thalli and zoospores of *Pontisma* are not strikingly different from those of *Sirolpodium*, the two genera are herewith merged, and the former genus is reduced to a synonym of the latter. *Petersenia* in a limited sense is also included in this family, because its thalli are frequently similar to those of *Sirolpodium*. Obviously, this arrangement also may be completely invalidated by future discoveries. As the family is herewith presented it includes two genera of incompletely known holocarpic species characterized by olpidioid or elongate and sometimes filamentous thalli which may or may not undergo segmentation. In some species the segments separate and become transformed directly into zoosporangia.

### SIROLPIDIUM

Petersen, 1905. Overs. Kgl. Dansk. Vids. Selsk. Forh. 5: 478.

*Pontisma*, Petersen, l.c., p. 482.

(PLATES 16, 17)

Thallus predominantly intramatrical but becoming partially extramatrical under certain conditions; olpidioid or elongate and filamentous; transformed directly into a single sporangium or undergoing separation and fragmentation to form a row of separate sporangia; fragmentation reduced or lacking in some species. Zoosporangia usually numerous in the host cell, variable in size and shape with one simple or branched exit tube which varies markedly in length and may extend considerably beyond the surface of the host wall, or occasionally opening within the host cell. Zoospores isocont with the flagella attached at or near the anterior end (?) and extending in opposite directions; swarming within the sporangia, emerging fully developed and swimming directly away; occasionally liberated within the host cell. Resting spore doubtful or unknown.

This genus was created by Petersen for de Bruyne's *Olpidium Bryopsidis* after he had found that the zoospores are biflagellate instead of uniflagellate. In the writer's opinion, *Pontisma* does not differ fundamentally from *Sirolpodium*, and on the basis of present-day knowledge it may well be merged with the latter genus. Sparrow ('34) maintained that it differs from *Sirolpodium* by its more irregularly tubular thallus and the fact that the segments do not separate and form isolated and free sporangia. Nevertheless, both he and Petersen report that in exceptional cases the thalli appear to fragment and give rise to free or loosely connected

sporangia as in *Sirolpidium*. This striking similarity becomes evident when figures 13 and 14, Plate 16, of *S. Bryopsidis* are compared with figures 4 and 5, Plate 17, of *S. (Pontisma) lagenidioides*. The tendency to greater or less fragmentation may well be a specific instead of a generic difference. Sparrow further reported that the zoospores are slightly different in the two genera, but his descriptions and figures of the positions of flagella are somewhat indefinite and unclear. Here also the differences may be only specific.

Infection of the host and the early developmental stages are not well known in all species, and the following account of these processes is based largely on *S. Bryopsidis*. As in *Eurychasma* and *Ectrogella*, the zoospore comes to rest on the host cell, encysts, and soon develops a germ tube which penetrates the host wall. Its content flows into the host cell, while the spore case and penetration tube are left behind and remain attached for some time after germination. According to de Bruyne, the young thallus (figs. 6-8, plate 16) very early develops a wall or membrane which thickens with age and shows a weak cellulose reaction when tested. The thallus may develop into an oval, pyriform, ellipsoidal sporangium or elongate into a tubular filament, become septate, and then fragment into a number of segments (figs. 11, 12, 13, plate 16). These fragments then develop into olpidioid sporangia of various sizes and shapes (figs. 14, 15, plate 16) and form one simple or branched exit tube of variable length. The latter may curve about in the host cell or penetrate the latter's wall and project for a long distance on the outside (fig. 1, plate 16). The same type of development apparently occurs in *S. lagenidioides* with the exception that the segments of the irregularly elongate thalli rarely separate.

The protoplasm of the thalli and incipient zoosporangia is glistening and refringent in appearance with numerous suspended globules (figs. 6-9, plate 16; figs. 4, 5, plate 17). When young the zoosporangia contain numerous small vacuoles (figs. 14, 15, plate 16; fig. 6, plate 17) which apparently flow together at maturity and form a large central one as in *Olpidiopsis*, *Pythiella*, and other similar genera. So far nothing is known about cytokinesis, but it is apparently accomplished by centrifugal cleavage furrows which progress from the border of the central vacuole to the periphery and thereby delimit uninucleate spore rudiments. The zoospores complete their development in the sporangium (fig. 1, plate 16) and become very active and motile before the tip of the exit tube deliquesces. According to Sparrow they swim directly away after emerging, but de Bruyne reported that in *S. Bryopsidis* they may pause for a few moments at the tip of the exit tube and become amoeboid. He also figured them as anteriorly uniflagellate and occasionally undergoing division (figs. 4, 5, plate 16). Petersen reported them to be uni- and biflagellate, but according to Sparrow they possess two flagella of equal length inserted at or near the anterior end (fig. 2,

plate 16). His figures of fixed and stained zoospores (fig. 3, plate 9), however, show the two flagella laterally attached. In *S. lagenidioides*, he reported that the two flagella appear to arise from the concave central region (fig. 2, plate 17), while in some zoospores they seem to be attached to the narrow anterior end (fig. 3, plate 17).

The presence of resting spores has not been demonstrated with certainty in *Sirolpidium*. In *S. Bryopsidis*, de Bruyne reported that the contents of oval and globular thalli may contract and become invested with a thick hyaline smooth wall (fig. 18, plate 16), and, according to Sparrow ('34) Petersen also observed occasional thick-walled spores which he believed relate to this species. So far none have been found in *S. lagenidioides*.

Unlike *Eurychasma* and *Eurychasmidium*, *Sirolpidium* does not cause enlargement of the infected cells. Furthermore, neither they nor adjacent healthy ones are stimulated to divide. The effects of the fungus are local and confined to infected cells. In the case of *Bryopsis* infected with *S. Bryopsidis*, heavily parasitized plants may be recognized by the presence of blackened areas along the fronds, which are apparently areas in which the cells have been killed. As the parasite increases in size the plastids turn greenish-brown in color and eventually become clumped together with the remainder of the degenerating protoplasm, according to de Bruyne's figures. *Sirolpidium lagenidioides*, on the other hand, appears to be a weak parasite or saprophyte on *Ceramium* and is capable of growth and development under conditions unfavorable to its host.

#### PLATE 16

##### *Sirolpidium Bryopsidis*

(Figs. 1, 4-9, 18 after de Bruyne, '90; fig. 11 after Petersen, '05; figs 2, 3, 10, 12-17 after Sparrow, '34.)

Fig. 1. Tip of *Bryopsis plumosa* branch with four zoosporangia containing zoospores; the exit tube of one sporangium is entirely intramatrical.

Fig. 2. Free hand drawing and interpretation of the zoospore showing tapering anterior end with a refractive globe and the ventral groove from which flagella apparently arise.

Fig. 3. Zoospore killed in osmic acid fumes.

Figs. 4, 5. Division of zoospores.

Figs. 6-8. Young thalli with numerous refractive globules.

Fig. 9. Elongate and branched thalli.

Fig. 10. Young stage of fragmenting thallus.

Fig. 11. Early stage of thallus division.

Fig. 12. Elongate thallus fragmenting; traces of old thallus wall connecting the fragments.

Fig. 13. Elongate fragmented thallus.

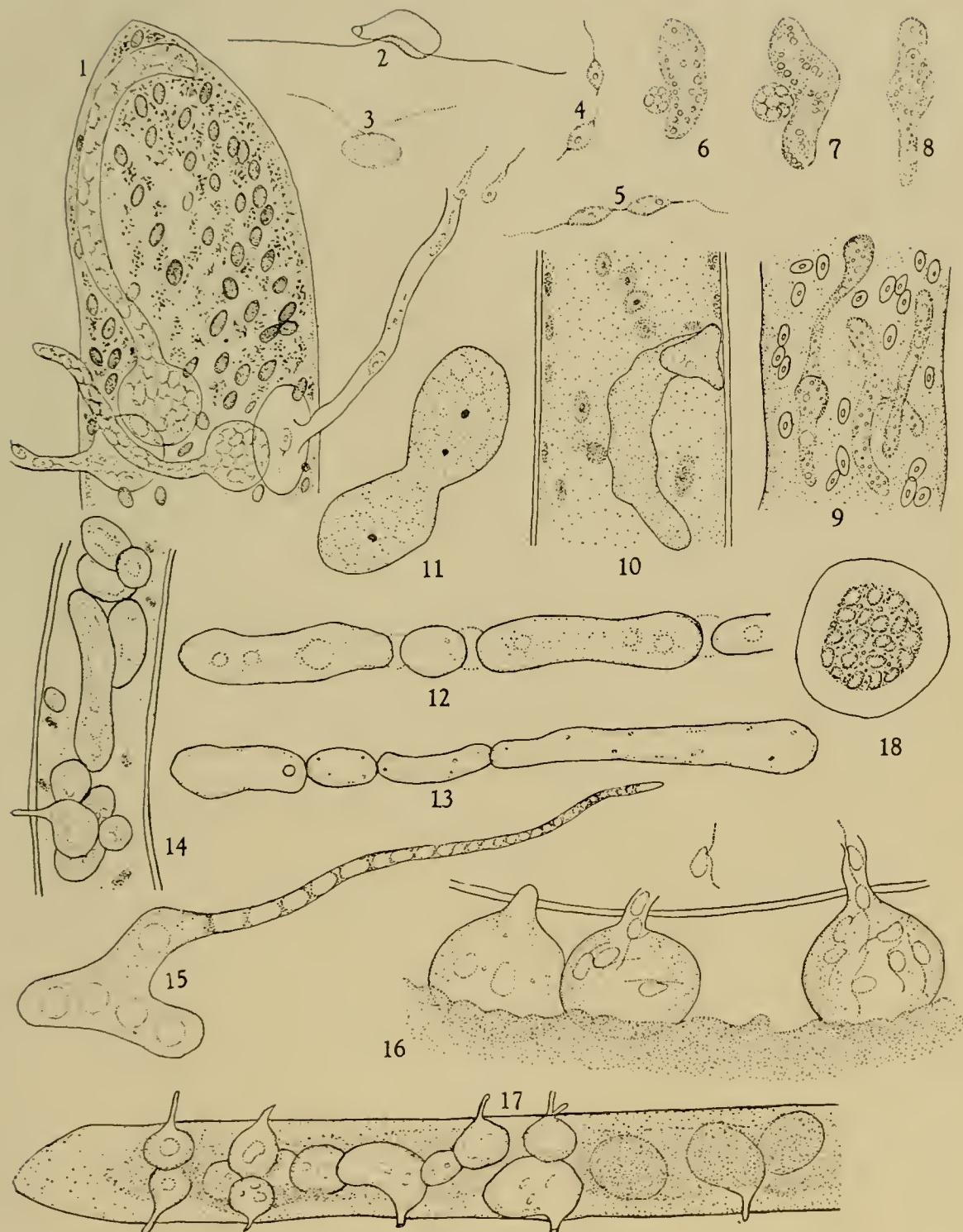
Fig. 14. Fragments becoming transformed into zoosporangia.

Fig. 15. Incipient, vacuolate, lobed zoosporangium with long exit tube.

Fig. 16. Emergence of zoospores from olpidioid sporangia.

Fig. 17. Tip of *Bryopsis* filament with numerous olpidioid sporangia.

## PLATE 16



Sirolpidium

**S. BRYOPSIDIS** (de Bruyne) Petersen, l.c., p. 479. Fig. XI, 1-8.  
*Olipidium Bryopsisidis* de Bruyne, 1890. Arch. Biol. 10: 85. Pl. 5, figs. 1-15.

Thallus usually intramatrial, becoming partially extramatrical under certain conditions; small, unicellular and olpidioid, or elongate, tubular and filamentous; frequently becoming septate and undergoing fragmentation into unicellular segments which develop into sporangia. Zoosporangia usually numerous in a cell, hyaline and smooth, spherical, oval, ellipsoid,  $12-17 \mu \times 13-38 \mu$ , elongate, cylindric, tubular,  $3-5 \mu \times 6-165 \mu$ . Zoospores narrowly pyriform and slightly arched,  $2 \times 4 \mu$ , with a refringent granule at the anterior end; flagella inserted near the anterior end (?). Resting spore (?) spherical, oval and elongate, hyaline and smooth, germination unknown.

Parasitic in *Bryopsis plumosa* in Italy (de Bruyne, l.c.), Denmark (Petersen, l.c.; Sparrow, '34) and Massachusetts, U. S. A. (Sparrow, '36); and saprophytic (?) in *Cladophora* sp., in Massachusetts, U. S. A. (Sparrow, l.c.).

In material studied at Woods Hole, Mass., Sparrow found that the growth of the thallus may be markedly influenced by environmental conditions. When the host is removed from its normal habitat and exposed only to dripping sea water the fungus grows out of the host and becomes distinctly filamentous and hypha-like. Sparrow found that additional extramatrical growth could be induced by transferring the infected material to solutions of low sugar concentrations. It is obvious from these preliminary culture studies that *S. Bryopsisidis* is highly variable in growth and development.

**S. LAGENIDIOIDES** comb. nov.  
*Pontisma lagenidioides* Petersen, l.c., figs. X, 1-3.

Thallus intramatrial, occasionally unicellular, lobed, curved and olpidioid; usually elongate, lobed, irregular and septate, frequently constricted at septa; rarely fragmenting into isolated segments. Zoosporangia hyaline and smooth, usually connected, occasionally free; oval, elliptical,  $13-15 \mu \times 14-16 \mu$ , elongate, cylindric,  $130-200 \mu$  in length, or irregular and slightly lobed. Zoospores pyriform and arched,  $2.5-3 \mu \times 4.5-7 \mu$ , with a refractive granule at one or both ends; flagella laterally inserted (?) on the concave side and oppositely directed; occasionally liberated within the host cell; motion erratic and tumbling in swimming. Resting spores unknown.

Weakly parasitic or saprophytic in *Ceramium rubrum*, *Ceramium* sp., *C. fructicosum*, *C. tenuissimum*, and *C. diaphanum* in Denmark (Petersen, l.c.; Sparrow, '34) and Massachusetts, U. S. A. (Sparrow, '36).

Sparrow reported that the zoospores of this species are strikingly similar to those of Butler's (l.c.) *Rozellopsis inflata*, and believed that on these grounds Butler's species shows affinities with *S.*

*lagenidioides* and species of *Olpidiopsis*. It is to be noted again, however, that the flagella of *S. lagenidioides* (fig. 3, plate 17) also appear to be attached to the narrow anterior end of the zoospores.

## PETERSENIA

Sparrow, 1934. Dansk. Bot. Ark. 8: 13.

(PLATE 18)

Thallus entirely intramatrial, unicellular, elongate, narrowly cylindric, irregularly lobed and contorted, rarely ellipsoid, and olpidioid; occupying one or more host cells. Zoosporangia solitary or numerous, variously shaped with 1 to 4 exit tubes of variable length. Zoospores laterally (?) biflagellate, isocont; flagella extending in opposite directions; developing completely and swarming in the sporangium before emerging, swimming directly away without any pause at the mouth of the exit tube. Resting spores doubtful or unknown.

This genus was established to include species of *Pleotrichelus* which were found to have biflagellate zoospores. It is not improbable that other marine species of the latter genus may also be transferred to *Petersenia* when their life cycles and method of development are completely known. *Petersenia andréei* is apparently a species of *Olpidiopsis* and is accordingly excluded from this genus which leaves only one valid species, *P. lobata*. The thallus of

## PLATE 17

### *Siroplidium lagenidioides*

(Fig. 1 after Petersen, '05; figs. 2-9 after Sparrow, '34.)

Fig. 1. Elongate irregular septate, constricted thallus with four exit tubes.

Fig. 2. Arched zoospores with a refractive granule at each end and two equal, laterally (?) attached flagella.

Fig. 3. Free hand drawing and interpretation of zoospores showing flagella attached near anterior end.

Fig. 4. Irregular septate thallus.

Fig. 5. Group of thalli showing "rudimentary fragmentation."

Fig. 6. Vacuolate sporangium with a branched exit tube.

Fig. 7. Curved elongate, continuous and solitary sporangium with quiescent zoospores.

Fig. 8. Emergence of zoospores.

Fig. 9. Empty loosely attached sporangia.

### *Blastulidiopsis chattoni*

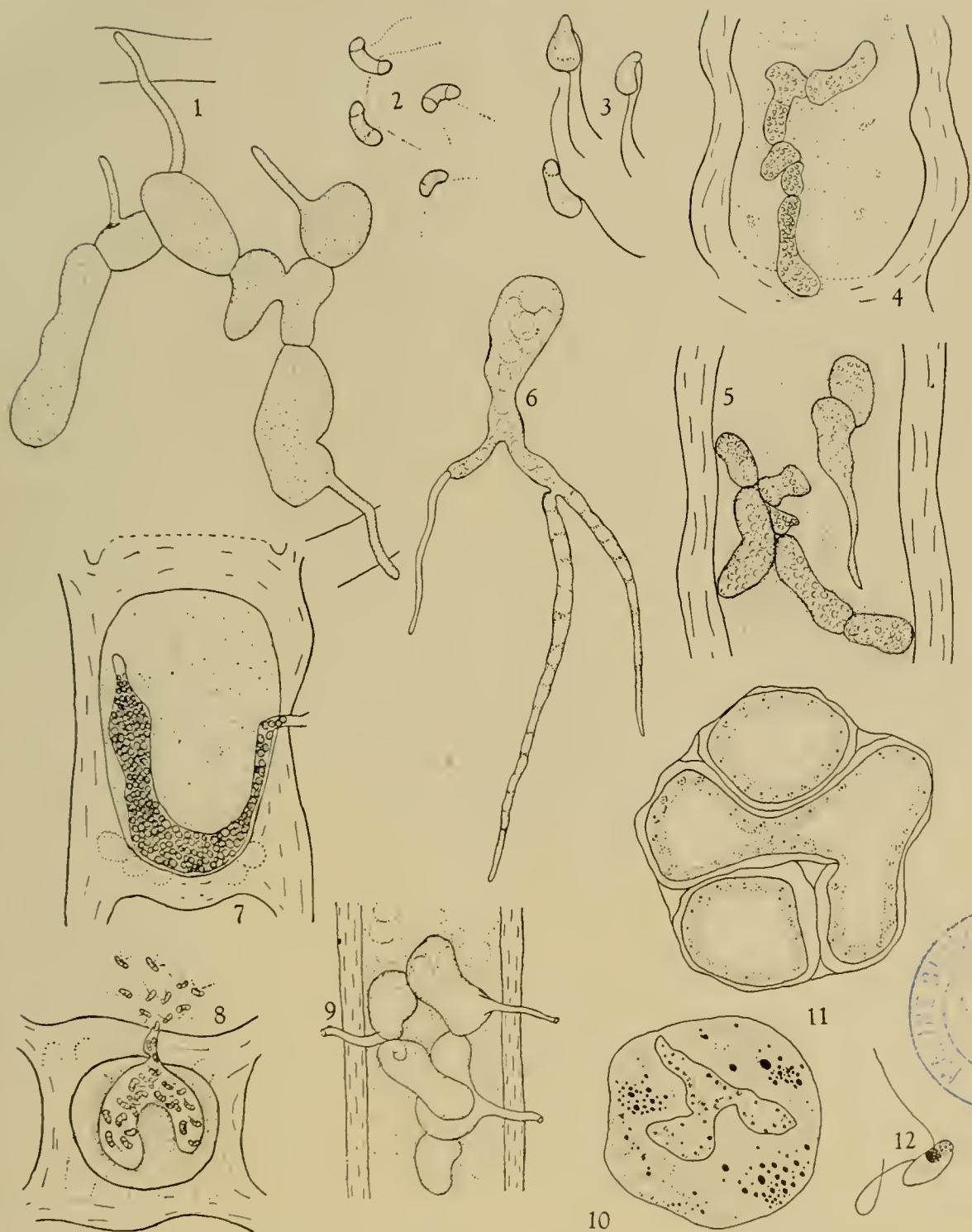
(All drawings after Sigot, '31)

Fig. 10. Young vacuolate lobed thallus in egg of *Cyclops*.

Fig. 11. Section of *Cyclops* egg showing lobes of sporangium in section; nuclei lying in a thin peripheral layer of cytoplasm.

Fig. 12. Laterally biflagellate isocont zoospore with nucleus near the center and a large refringent body at the anterior end.

## PLATE 17



Sirolpidium, Blastulidiopsis

this fungus may be strikingly similar in appearance to those of species of *Sirolpodium*, with the exception that it does not become septate and fragment into segments. Should the latter characters prove insignificant in generic diagnoses and phylogeny, *Petersenia*, in the present sense, may perhaps be merged with *Sirolpodium*. On the other hand, the olpidioid thalli bear a strong resemblance to those of *Olpidiopsis*, particularly to *O. irregularis*, according to Sparrow ('34).

Zoospore germination and infection of the host have not been observed in this genus, but these processes are probably similar to those of *Sirolpodium*, *Ectrogella*, etc. Sparrow ('34) reported that in the early stages the thallus is "somewhat plasmodial in nature" but he did not illustrate any of the initial developmental phases. At maturity, however, a well-defined wall is present which stains a dark, ruby color when tested with chloro-iodide of zinc. As noted previously the thallus varies markedly in size and shape (figs. 3-8). Within the tetraspores of the host it usually assumes the shape of the confining cell (fig. 4), but even under such conditions lobed specimens may occur, as Feldman ('40) has shown. In the vegetative state the protoplasm is refractive and vacuolate (figs. 4, 7), and as the thallus is transformed into a sporangium, the small vacuoles presumably flow together and form one or more larger central ones. The late stages of cleavage and sporogenesis closely resemble those of *Pythium*, according to Sparrow. The incipient spore initials undergo an individual rocking movement which becomes more pronounced as they separate and acquire their mature form. At the same time traces of flagellar motion become visible at the periphery of the spore mass, and this increases in intensity until the zoospores are mature and swarming within the sporangium. As the tip of the exit tube deliquesces they emerge (fig. 3) and swim directly away. According to Sparrow, the zoospores (figs. 1, 2) are elongate, pyriform, shallow-grooved, and contain a refractive body at the anterior end. The flagella are reported to be inserted laterally, but some of Sparrow's figures suggest that they arise near the anterior end.

**P. LOBATA** (Petersen) Sparrow, I.e., p. 13, pl. 2, figs. 1- $N$ ; 1936. Biol. Bull. 70: 245. Pl. 2, figs. 1, 2.

*Pleotrichelus lobatus* Petersen, I.e., p. 460, figs. V, 1-7.

Zoosporangia solitary or numerous, often occupying more than one host cell, or filling it completely and conforming to the latter's size and shape; usually markedly and irregularly lobed, elongate and tubular, or oval, ellipsoid and olpidioid with 1 to 3 simple or branched exit tubes of variable length. Zoospores elongate, pyriform, slightly arched and shallow-grooved,  $3 \times 4.5 \mu$ . Resting spores unknown.

Parasitic in the vegetative cells and tetraspores of *Spermothamnion turneri*, *S. repens*, *Callithamnion corymbosum* and *C. hookeri*, in Denmark (Petersen, I.e.; Sparrow, I.e.), *C. roseum* in Massachusetts,

U. S. A. (Sparrow, '36) and in the disporangia of *Seirospora interrupta* near Villefranche-sur-mer in the Mediterranean (J. and G. Feldman, '40).<sup>1</sup>

This species may occur in whitened and dead cells of its hosts which suggests that it is only weakly parasitic. According to Sparrow, it is not assisted by other organisms in the early stages of invasion, but in old infections, bacteria and protozoa are always present and aid in the destruction of the content of the host cell.

Whether or not *Pleotrichelus pollagaster* Petersen (figs. 9-11) belongs in *Petersenia* is questionable. Sparrow ('34) included it provisionally in this genus, because he found its zoospores to be similar in shape and size to those of *P. lobata*. He did not, however, determine the number and position of the flagella, and until these points have been conclusively settled the exact generic position of *P. pollagaster* will remain doubtful.

Sparrow ('36) found two other fungi which he assigned tentatively to *Petersenia* as unidentified species. One occurred in the eggs of a microscopic animal, possibly a rotifer, adherent to filaments of *Ceramium diaphanum*. The parasite filled the whole interior of the egg (fig. 12) and was transformed at maturity into a sporangium,  $20 \times 50 \mu$ , with 1 to 3 short broad,  $8 \mu$  in diameter, exit tubes. The formation and emergence of the zoospores were not observed, although a number of the spores which had failed to emerge were found within sporangia. These bodies were reniform, "of the laterally biciliate type,"  $2 \times 4 \mu$ , and resembled the zoospores of

<sup>1</sup> Bull. Soc. Hist. Nat. Afrique Nord 31: 72.

#### PLATE 18

(Figs. 1-6, 11-14 after Sparrow, '34, '36; figs. 7-10 after Petersen, '05. Figs. 13, 14 drawn from photographs.)

##### *Petersenia lobata*

Fig. 1. Group of isocont zoospores; point of attachment of flagella uncertain.

Fig. 2. Freehand, enlarged drawing and interpretation of zoospore.

Fig. 3. Emergence of zoospore from olpidioid zoosporangium.

Fig. 4. Infected tetraspores of *Spermothamnion*.

Fig. 5. Olpidioid and nodular thalli.

Fig. 6. Irregular thallus with four short branches.

Fig. 7. Elongate, lobed and constricted multivacuolate thallus occupying two host cells.

Fig. 8. Empty zoosporangium.

##### *Pleotrichelus (Petersenia) pollagaster*

Fig. 9. Lobed thallus with three long exit tubes.

Fig. 10. Olpidioid sporangium.

Fig. 11. Irregular resting spore.

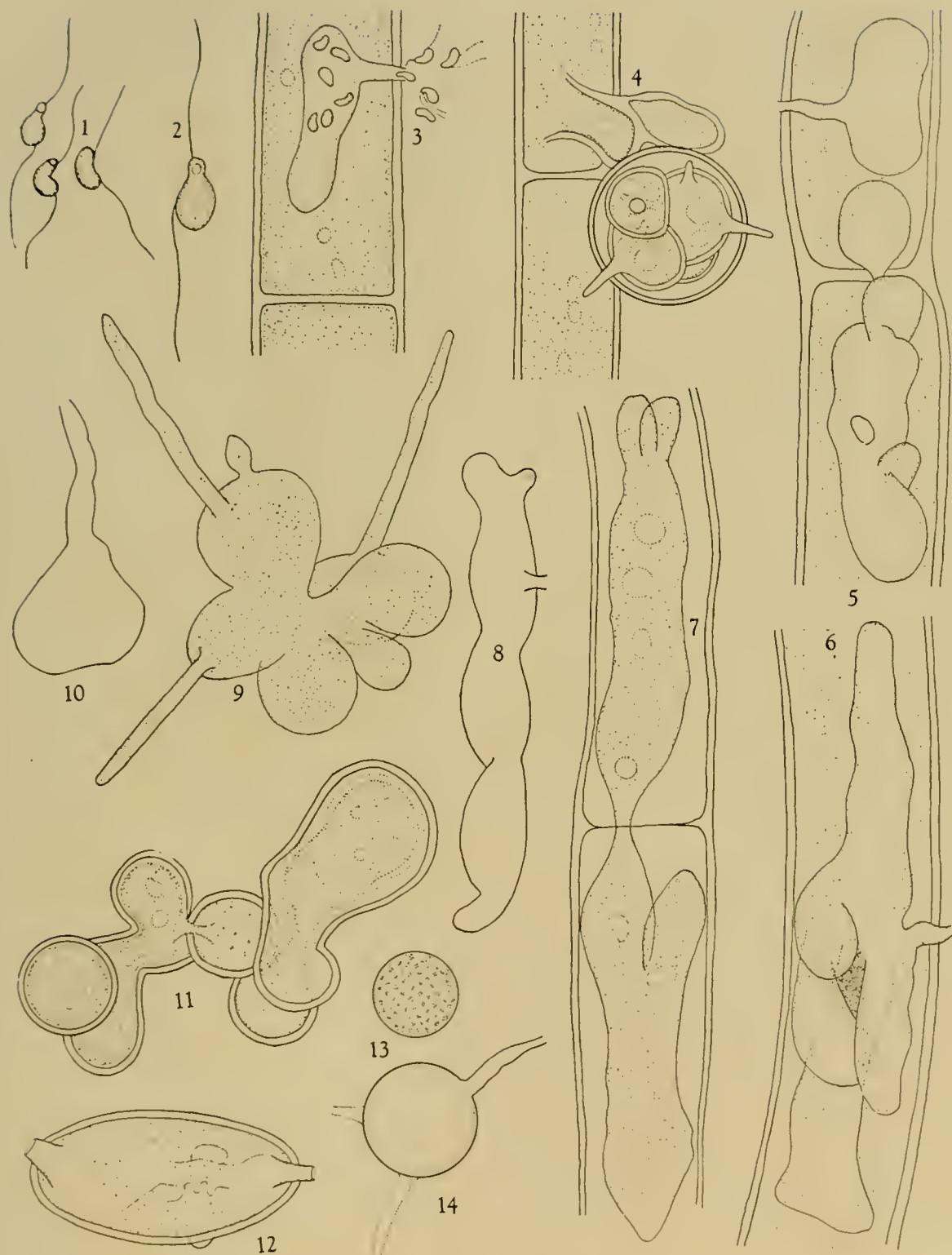
##### *Petersenia* sp.

Fig. 12. Sporangium in rotifer (?) egg with two bi-flagellate isocont zoospores.

Fig. 13. Young thallus of *Petersenia* sp. saprophytic in *Ceramium diaphanum*.

Fig. 14. Empty zoosporangium with three exit tubes.

## PLATE 18



*Pythium*. The other unidentified species occurred as a saprophyte in *Ceramium diaphanum* which had been kept in a laboratory aquarium for several weeks. One to several spherical (figs. 13-14) and irregular thalli of variable size, 20-96  $\mu$  in diameter, were found in a single internode. Each thallus de-

veloped into a sporangium at maturity with up to ten or more radiating, narrow tapering exit tubes, 7  $\mu$  in diameter, which penetrated the host cell wall. Zoospores and resting spores were not observed, and it is accordingly uncertain whether or not this species belongs in *Petersenia*.

## Chapter VI

### Lagenidiaceae

Schroeter, 1897. Engler und Prantl, Die Nat. Pflanz'f. I, 1: 88.

THIS FAMILY includes a number of saprophytes and parasites of algae, higher plants, nematodes, insects, and other animals which are characterized primarily by reniform, laterally biflagellate zoospores, and sexually formed resting spores. The family was formerly included in the Anecylistales, but in light of Miss Berdan's ('37, '38) discovery that *Ancylistes* is a genus of the Entomophthorales, the name Anecylistales is no longer tenable. Accordingly, in 1939 the author raised the family Lagenidiaceae to ordinal rank, and since that time Sparrow ('42) has included the Olpidiopsidaeae, and Sirolpidiaceae as well as the Lagenidiaceae in this order. Whether or not these families constitute a distinct order of equal rank with the Saprolegniales, Leptomitales, Peronosporales, etc., is very questionable. According to Sparrow's interpretation the Lagenidiales include species with iso- and heterogamous types of reproduction as well as iso- and heterocont zoospores, and as such it obviously cannot be regarded as more than a temporary and convenient expedient of classification. In view of our lack of knowledge relative to many of the species, genera, and families included in this order, it is perhaps wiser for the time being to avoid placing the Olpidiopsidaeae, Sirolpidiaceae, and Lagenidiaceae in a distinct order.

The thallus of the Lagenidiaceae varies from a simple ovoid, unicellular, *Olpidium*-like cell to an extended filamentous, branched, septate mycelium which may be confined to a single host cell or occupy several cells. These parasites and saprophytes gain entrance into the host by an infection tube from germinating zoospores. The thallus develops as an extension and enlargement of the tip of the germ tube and soon becomes long and filamentous or enlarges into a globular, oval, lobed, and irregular structure. It may remain unicellular and continuous in some species or divide transversely into several segments. With further growth these segments may become oval, ellipsoid, and spherical, making the thallus deeply lobed at the septa, or they may remain cylindrical with little or no constrictions in the region of the cross walls. At maturity these segments are holocarpically transformed either into sporangia or slightly differentiated gametangia. In all

species which have been tested the walls of the thallus give a marked positive cellulose reaction. The protoplasm, particularly in *Lagenidium* and *Myzocytium*, usually includes a large number of refractive globules of various sizes, which give it a characteristic refringent and gleaming appearance, but at maturity and as sporogenesis begins it becomes more greyish granular.

In the majority of species the content of the sporangium emerges as a globular mass from the exit tube and undergoes cleavage into zoospores on the outside in much the same manner as in *Pythium*. The presence of a vesicular membrane around the protoplasmic mass and the zoospores which are subsequently formed has been reported in a number of species, but appears to be lacking in others. There is considerable disagreement in the literature about the presence of this structure, and further intensive study of its occurrence in the Lagenidiaceae is needed. In a few species the zoospores are completely developed in the sporangium, emerge, and swim directly away, or they are discharged prematurely, come to rest in a mass and complete their development on the outside. In other species they encyst in a loose mass at the mouth of the exit tube as in *Achlya* and exhibit marked diplanetism. It is accordingly obvious that the process of zoosporegenesis and the initial behavior of the zoospores vary from the *Olpidiopsis* to the *Pythium* and *Achlya* types. The zoospores throughout the family are predominantly reniform and somewhat pyriform in shape, and in some species a distinct ventral groove is present in which the flagella are inserted. Heterocont zoospores have been reported in two species.

Sexual reproduction is predominantly heterogamous, but in *Lagena* and *Resticularia* it is reported to be isogamous. Isogamy is present in *Lagenidium sacculoides* also, according to Serbinow ('07). The segments of elongate thalli, as well as entire unicellular thalli, which function as male and female gametangia are only slightly or not at all differentiated as sexual organs. They may occur among the sporangia in the same thallus or in separate thalli, but the presence of heterothallism has not been definitely proven. No monozoospore cultures and infec-

tions have yet been made to determine whether the zoospores carry the potentialities of one or both sexes. In some of the unicellular species separate thalli may function as male and female gametangia, but it has not been proven that they represent distinct male and female strains. In light of our meager present-day knowledge it would be premature to discuss homo- and heterothallism in the Lagenidiaceae.

In some species the unicellular thallus may divide at maturity into two cells which then function as male and female gametangia, respectively. In most species, however, the female gametangium is usually larger, more vesicular, and frequently barrel-shaped, while the so-called antheridium is usually elongate and tubular. In *Lagena*, as noted before, the unicellular thalli which fuse are equal in size and indistinguishable. For this reason, the terms oogonia and antheridia may be used only tentatively and with reservation for the sexual organs in the Lagenidiaceae. Differentiation of an egg cell and periplasm in the female gametangium has not been convincingly demonstrated, but the ooplasm may contract and aggregate toward the conjugation tube or pore during plasmogamy. Shortly before fusion a connecting pore is formed between the two gametangia, or the antheridium forms a tube or canal which projects into the oogonium. In *Lagena*, however, the tube fuses with the surface of the oogonium without entering it. The content of the antheridium then slowly flows into the oogonium and fuses with the ooplasm, after which the zygote becomes invested with a thick wall. The resting spore thus formed lies free in the oogonium, resembles the oospore of the higher Oomycetes, and is generally referred to in the literature as an oospore. In some species the antheridium is lacking, with the result that the resting spores are formed parthenogenetically.

The cytology of sexual reproduction from fixed and stained material has been studied in only one species, and very little is known about the gametic nuclei and their behavior during plasmogamy and karyogamy in the family as a whole. Until more is known about these developmental phases the relationships of the Lagenidiaceae with the Saprolegniales and Peronosporales will remain obscure.

As it is herewith presented the Lagenidiaceae includes *Lagenidium*, *Myzocytium*, and *Lagena*. The first two genera are very similar and appear to be closely related, and in light of present-day knowledge it is questionable whether they should be separated. As Cook ('35) has already noted, the differences are perhaps only specific instead of generic. *Lagenidiopsis* is merged with *Lagenidium*, while *Achlyogoton* and *Mitochytridium* are excluded because of their uniflagellate zoospores. *Resticularia* is listed as doubtful genus, but it may possibly prove to be identical to and synonymous with *Lagenidium*. Its reported isogamous and zygomycetous type of sexual reproduction is very similar to that of *L. sacculoides*. On the other hand, future studies and discoveries may necessitate the inclusion of *Lagena*,

*Resticularia* and *L. sacculoides* in a separate family because of their characteristic method of sexual reproduction. *Protascus* is excluded from the Lagenidiaceae because of its lack of zoospores. A full description and illustration of this genus is nevertheless presented here to emphasize again to mycologists the priority of Dangeard's *Protascus* over the same generic name proposed by Wolk ('13) for another fungus.

Gaumann and Gaumann and Dodge included *Ectrogella* in the Lagenidiaceae, but subsequent workers have not followed this viewpoint. The presence, however, of isocont primary zoospores with flagella inserted just below the anterior end and laterally biflagellate heterocont secondary swarm-spores indicates a closer relationship, as Scherffel has pointed out, with the Saprolegniaceae. Tokunaga included *Aphanomyopsis* in this family on the grounds that it lacks a typically developed mycelium and is holocarpic. The shape, structure, size and general appearance of the thallus and zoospores are strikingly like those of the Lagenidiaceae, and in the encystment of the swarm-spores in a cluster at the mouth of the exit tube this genus is similar to *L. Oedogonii*. Furthermore, the locally paunchy cell in which the asexual or possibly parthenogenetic resting spore is formed is quite like the oogonium in species of *Lagenidium*. There is thus good structural evidence to support Tokunaga's viewpoint. Whether certain stages of Borzi's *Rhizomyxa* belong here is also problematical. Its reported mode of sexual reproduction is nonetheless strikingly similar to that of *Lagenidium* and *Myzocytium*, with the exception that an egg cell and periplasm are formed before fertilization occurs. In the latter character it is somewhat similar to *Pythiella*.

## LAGENIDIUM

Schenk, 1859. Verh. Phys. Med. Ges. Würzburg  
9: 27.

*Lagenidiopsis* de Wildeman, 1896. Ann. Soc.  
Belg. Micro. 20: 109.

(PLATES 19, 20)

Thalli intramatrical, solitary or numerous, confined to one cell or extending through several host cells; frequently elongate, straight, crooked, curved, irregular, coiled, tubular, hypha- and mycelium-like, with numerous blunt protuberances; lobed, branched or unbranched, slightly constricted or unconstricted at the cross walls; multicellular or unicellular, the latter continuous, globular, oval, ellipsoidal, sac-like and irregular; often attached to the host cell wall by the infection tube and zoospore case; holocarpic, transformed into sporangia or gametangia at maturity. Sporangia of the same shape and size as the individual segments and unicellular thalli, with one to several exit tubes of vary-

ing length, diameter, contour, and shape; content of sporangium usually emerging to form a globular mass at the mouth of the exit tube. Zoospores bean-shaped, reniform and somewhat pyriform, laterally biflagellate, with several small refractive globules, mono- or diplanetic; primary swarmers isocont, secondary swarmers heterocont; formed (1) extramatrically by progressive cleavage of the extruded globular mass of protoplasm which may be naked or surrounded by a vesicular membrane as in *Pythium*; (2) delimited in the sporangium, emerging singly and completing development at the mouth of the exit tube; or (3) completely developed in the sporangium, emerging in succession and swimming directly away. Antheridia borne on the same or different thalli; oogonia terminal or intercalary, variously shaped; differentiation of egg cell or oosphere prior to fusion absent or very doubtful; epiplasm lacking; content usually contracting toward the conjugation canal during plasmogamy. Antheridia when present usually more slender, elongate and cylindrical, frequently forming a conspicuous perforation and conjugation tube which extends into the oogonium; fused protoplasts contracting and becoming invested with a definite wall. Oospores sexual or parthenogenetic, lying free in the oogonium, usually spherical, oval or ellipsoidal, smooth or warty, hyaline or colored, thick-walled with one or more large refractive globules; germinating by giving rise directly to biflagellate zoospores.

This is the largest genus of the family and includes approximately fifteen species, some of which are doubtful, incompletely known, and possibly synonymous. The majority are parasites of algae; two occur in tissues of higher plants, and two live in the body of insects. A number of species occur on the same host and are structurally similar. It is thus probable that when extensive cross inoculations have been made and the range of variation of the individual species is known some of them will prove to be identical. As to geographic distribution, they have been reported from Asia, Europe, and North America.

As is shown in figure 1, the zoospores come to rest on the host cell and penetrate it by a germ tube of varying length and diameter, tip of which enlarges as the content of the spore passes into it. This tip soon elongates into a comparatively thick hyphal-like tubular strand as in *L. rabenhorstii* (figs. 2-4) or enlarges into a globular, oval, vesicular, sac-like and somewhat irregular structure as in *L. brachystomum*, *L. enecans*, *L. Oedogonii*, etc. (figs. 30, 39, 45, 49). This enlargement of the tip eventually develops into the mature thallus and in several species is attached to the host wall by the persistent zoospore case and infection tube. With further growth and increase in diameter, the thallus of the more extensive and elongate species develops a few side branches and numerous protuberances which often make it very irregular and crooked. As its ends approach the limits and cross walls of the host, they may either penetrate into adjacent cells or double

back in the same cell (fig. 34). Very shortly transverse septa are formed at more or less regular intervals in such thalli, and they thus are divided into a linear series of elongate, cylindrical or irregular segments. In some species like *L. Closterii*, *L. marchalianum*, *L. giganteum*, etc. (figs. 34, 37, 54) the thallus is quite narrow, mycelioid and *Pythium*-like, while in *L. pygmaeum*, *L. Cyclotellae*, *L. Oedogonii*, and *L. oophilum* it may be reduced to a single globular cell as in *Olpidium* (figs. 25, 39, 49, 60).

The protoplasm of the thallus includes numerous fairly large refractive bodies which give it the whitish, refringent gleam characteristic of the family Lagenidiaceae. In addition several small vacuoles are usually present. The segments of the thallus or whole thalli are transformed directly into sporangia, oogonia and antheridia. In the case of sporangia the small vacuoles may run together to form a large central one by the time the exit tubes have developed. As sporogenesis approaches, the large refractive bodies apparently break up into smaller fragments and become highly dispersed, so that the protoplasm loses much of its refractive appearance and becomes more greyish granular. The exit tubes vary considerably in length, diameter, shape, contour, and the extent to which they project beyond the host wall. They may be inflated at the base or just before they pass through the host wall, constricted or unconstricted, straight, curved, irregular or tortuous, and end almost flush with the surface of the host, or extend considerably beyond it.

In all species except *L. pygmaeum*, *L. Cyclotellae*, and *L. oophilum* the protoplasm of the sporangium is reported to emerge at maturity and form a spheri-

#### PLATE 19

##### *Lagenidium rabenhorstii*

(Figs. 1-14, 16 after Zopf, '84; figs. 15, 17 after Cook, '35; figs. 18-22 after Wildeman, '96.)

Fig. 1. Early infection stages of *Spirogyra* cells.

Figs. 2-4. Successive developmental stages of thallus.

Fig. 5. Sporangium with emerged contents surrounded by a membrane.

Figs. 6-8. Successive stages of cleavage and maturation of the zoospores.

Fig. 9. Small, reduced thallus with zoospores swarming in a vesicle.

Fig. 10. Mature zoospore.

Figs. 11-14. Stages in fusion of the contents of antheridium and oogonium.

Fig. 15. Prefusion stage showing differentiation of an egg cell in the oogonium.

Fig. 16. Mature oospore in oogonium of an elongate thallus.

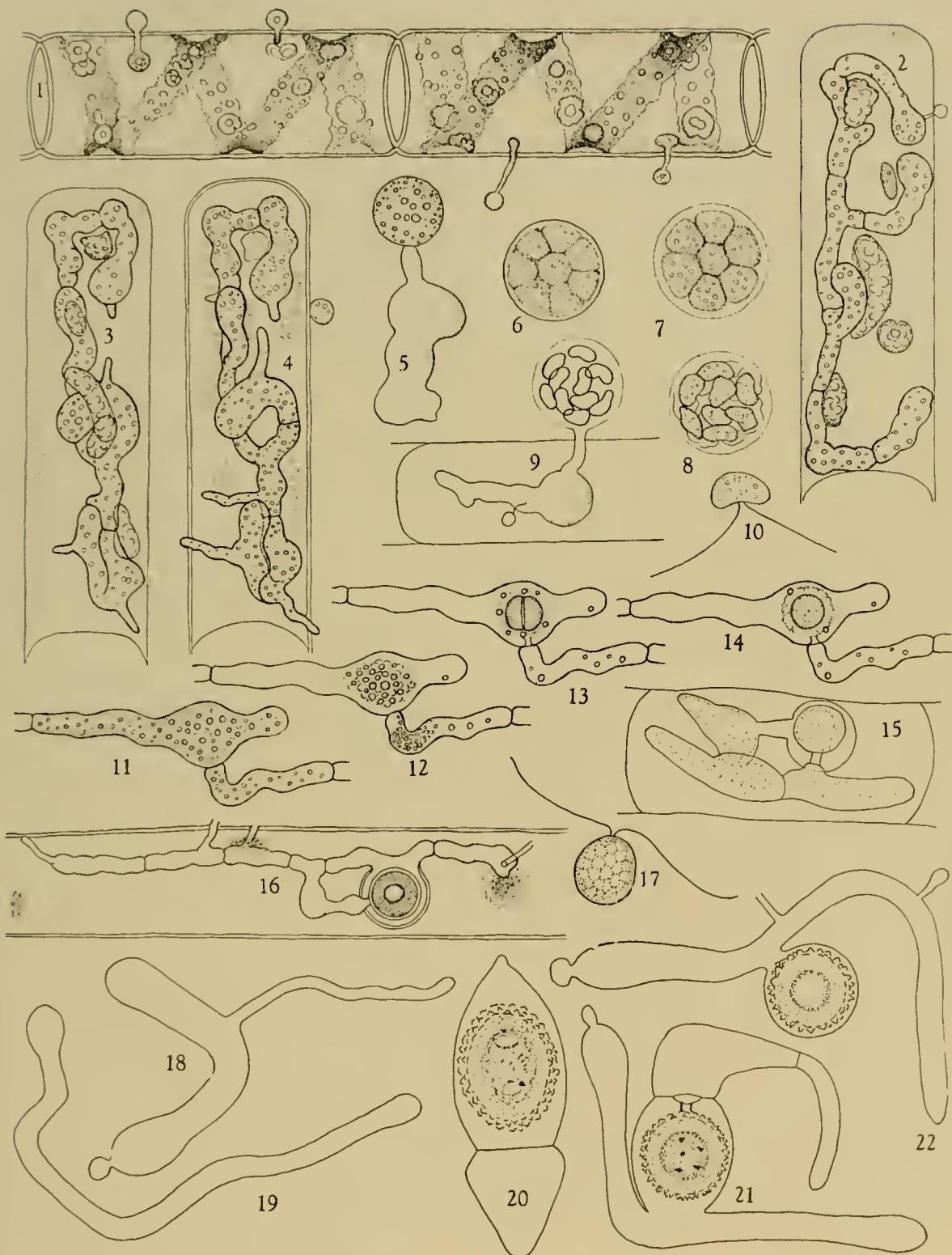
Fig. 17. Single, large zoospore produced by germinated oospore.

##### *Lagenidium (Lagenidiopsis) reductum*

Figs. 18, 19. Young and elongate unicellular thalli.

Fig. 20. Antheridium, oogonium, and warty oospore.

## PLATE 19



Lagenidium, Lagenidiopsis

cal, oval or slightly irregular, globular mass at the mouth of the exit tube. As will become more evident in the diagnoses of individual species, investigators are not in agreement as to whether this mass is naked or enclosed in a definite membrane as in *Pythium*. According to present data the latter is apparently present in some species and lacking in others, but a careful restudy of this structure is necessary before the problem is settled. The protoplasmic mass may be vacuolate and undergo marked rocking or oscillating movements shortly after emerging, and in some instances it may even move or be carried away from the exit tube. In *L. giganteum* the protoplasm may occasionally emerge in several separate masses, according to Couch ('35). Cleavage begins very soon, and in most species it appears to be progressive and centripetal. In the masses which possess a large central vacuole, i.e., *L. Oedogonii* and *L. giganteum*, cleavage is largely centrifugal in direction. While cleavage is going on the slow oscillating or rocking movement continues, and as the process is completed and flagella develop at the outer periphery of the individual segments, and this motion is augmented by that of the rudimentary zoospores. Cleavage stages in *L. giganteum* have been intensively studied at different time intervals by Couch. As the protoplasm emerges it includes one or more large central vacuoles and numerous small peripheral ones (fig. 55). The central vacuoles fuse (fig. 56), but the peripheral ones remain intact and are eventually included in the zoospores. Flagella in pairs are formed on the periphery of the mass opposite the small vacuoles, and shortly thereafter cleavage furrows develop centrifugally from the central vacuole and divide the mass into biflagellate, univacuolate segments. The central vacuole collapses as the furrows reach the periphery, and as a result the zoospore mass contracts (fig. 57). The zoospores soon begin to oscillate individually and glide upon each other as they mature, and within a few minutes they are actively swarming in a localized and restricted region (fig. 58). It is this localized swarming in numerous other species which suggests or indicates the presence of a retaining membrane, although it often cannot be clearly seen. Shortly thereafter the swarmspores separate very quickly as if they had been freed by the rupture or deliquescence of the membrane. In species where no membrane occurs, the zoospores pull apart more gradually as they mature, and soon swim away.

In *L. pygmaeum* and *L. oophilum* the incipient zoospore segments are delimited in the sporangium, emerge in succession, and complete their development near the mouth of the exit tube, while in *L. Cyclotellae* they are developed completely in the sporangium, emerge singly, and swim directly away, according to Scherffel ('25). *Lagenidium Oedogonii* is particularly interesting and significant relative to its zoospores. They may develop either extramurally in a vesicle, as in *Pythium*, or within the sporangium. In the latter case they collect in a cluster at the mouth of the exit tube after emerging

## PLATE 20

Figs. 23, 24. Irregular contorted thalli of *L. entophysum* with smooth and warty oospores. Zopf, '84.

Fig. 25. Olpidium-like thallus of *L. pygmaeum* with partially formed zoospores emerging in a vesicle. Zopf, '87.

Figs. 26, 27. Encysted and motile zoospores of *L. pygmaeum*. Zopf, l.c.

Figs. 28, 29. Mature oospores of *L. pygmaeum*. Zopf, l.c.

Fig. 30. Empty thallus of *L. enecans* from a *Cymatoplera solea* cell. Scherffel, '25.

Figs. 31, 32. Heterocont secondary swarmers or zoospores of *L. enecans*. Scherffel, l.c.

Fig. 33. Oospores, *L. enecans*. Scherffel, l.c.

Fig. 34. Portion of filamentous thallus of *L. Closterii*. Couch, '35.

Fig. 35. Inflation of exit tube before passing through host wall. Couch, l.c.

Fig. 36. Zoospore of *L. Closterii*. Couch, l.c.

Fig. 37. Thallus of *L. marchalianum* in *Oedogonium* cell. Couch, l.c.

*L. Oedogonii*

Fig. 38. Germinated zoospore and cellulose plug formed around germ tube. Couch, l.c.

Fig. 39. Unicellular thallus transformed into a zoosporangium with contents beginning to emerge. Couch, l.c.

Fig. 40. Vacuolate content of sporangium after emerging. Couch, l.c.

Figs. 41, 42. Side and ventral views of heterocont, secondary swarmers or zoospores. Scherffel, l.c.

Fig. 43. Encysted zoospores at mouth of exit tube. Scherffel, l.c.

Fig. 44. Oospore. *L. brachystomum*. Scherffel, l.c.

Fig. 45. Elongate, unbranched thallus from *Gomphinema* cell. Scherffel, l.c.

Fig. 46. Zoospores in a vesicle. Couch, l.c.

Fig. 47. Zoospore. Couch, l.c.

Fig. 48. Oospore. Scherffel, l.c.

*L. Cyclotellae* Scherffel, '25

Fig. 49. Olpidium-like thallus undergoing cleavage.

Fig. 50. Zoospore.

Fig. 51. Oospore.

*Lagenidium* sp. Couch, '35

Fig. 52. *Lagenidium* sp., in *Oedogonium*. Couch, l.c.

Fig. 53. Diplanetic zoospores.

*L. giganteum* Couch, '35

Fig. 54. Portion of filamentous thallus.

Fig. 55. Vacuolate content of sporangium shortly after emerging.

Fig. 56. Early stage of sporogenesis; flagella arising adjacent to peripheral vacuoles.

Fig. 57. Later contracted stage following disappearance of central vacuole; peripheral vacuoles incorporated in the zoospores.

Fig. 58. Zoospores in a vesicle.

Fig. 59. Various views of the zoospores.

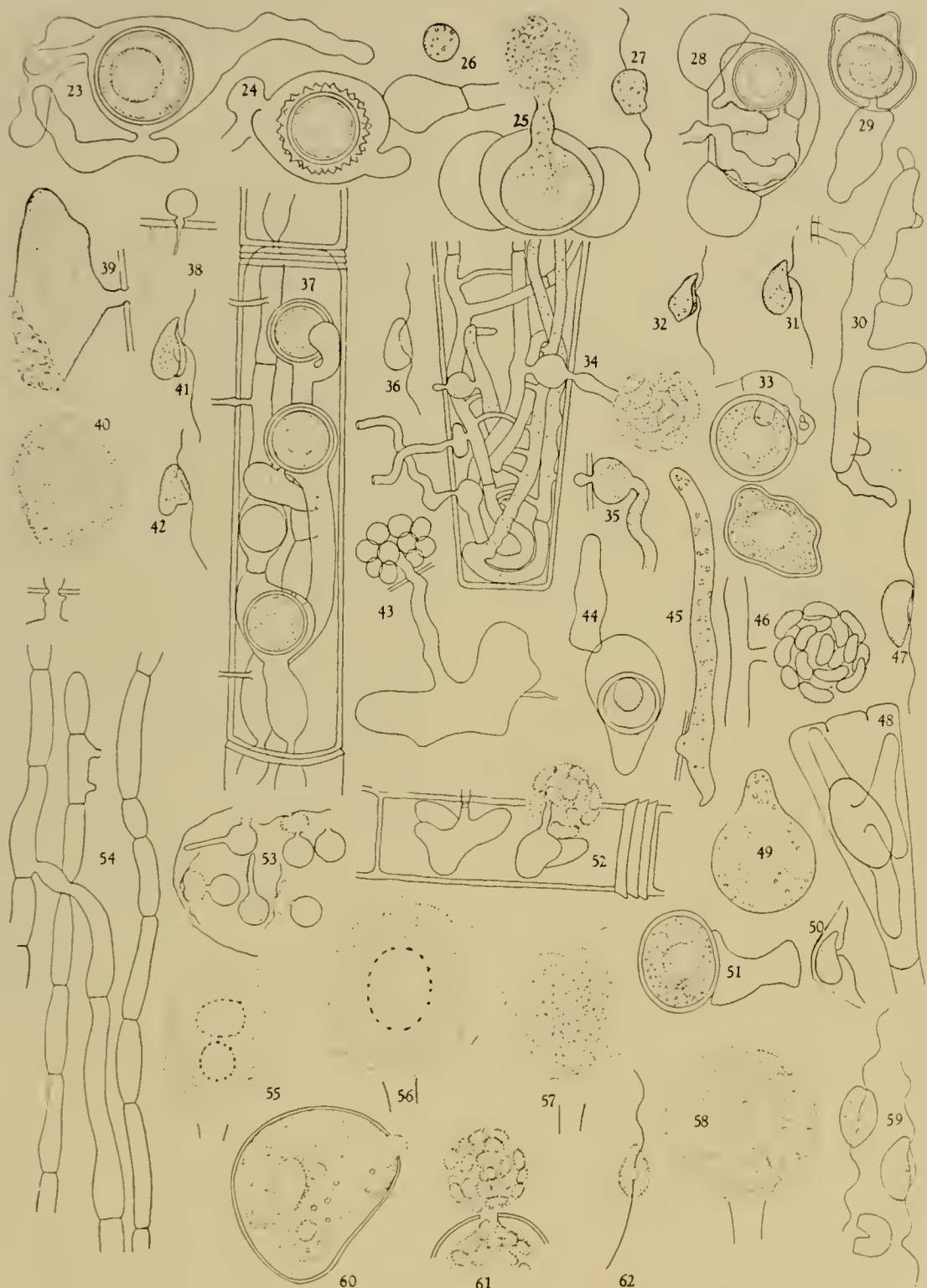
*L. zoophthorum* Sparrow, '39

Fig. 60. Lobed thallus in rotifer egg.

Fig. 61. Emergence of zoospores.

Fig. 62. Zoospore.

## PLATE 20



Lagenidium

and encyst (fig. 43), later germinating and leaving a hyaline shell behind as in *Achlya*, *Ectogella*, etc. Diplanetism has also been shown by Scherffel and Couch to occur in *L. enecans* and *Lagenidium* sp. (figs. 52, 53). It is thus obvious that species of *Lagenidium* may exhibit a wide range of variation in place and time of sporogenesis and zoospore behavior.

The zoospores are generally described as bean-shaped, but in species which have been critically studied this appears to be the initial shape only. As they grow older they become more pyriform and reniform with a pointed anterior and a rounded posterior end and a ventral groove. The flagella are inserted laterally in this depression, and in most species they have been figured as equal in length. The secondary swarmers in *L. enecans* and *L. Oedogonii* (figs. 31, 32, 41, 42), however, are heterocont with the shorter flagellum extending forward, according to Scherffel ('25), but in *Lagenidium* sp., Couch illustrated them as isocont (fig. 53). Their method of swimming is rather smooth and regular in contrast with the darting movement of the chytrid swarmspores, and in this respect they are very similar to those of *Achlya*, *Saprolegnia*, etc.

The antheridia and oogonia may occur in the same thallus and among the sporangia (fig. 16) or in separate thalli. The elongate multicellular thalli more often bear both gametangia. In the small unicellular species the thallus is usually divided by a transverse septum into two cells at maturity, which become the so-called antheridia and oogonia, respectively, while in other reduced species conjugation may occur between separate unicellular thalli. Species in which both gametangia are borne on the same thallus have been generally referred to as monoecious, while those in which the respective gametangia are borne on separate thalli are regarded as dioecious. It is not known and has never been demonstrated, however, whether the so-called dioecious thalli have arisen from zoospores of the same or different sporangia and thus represent distinctly male and female strains. Until monozoospore studies have been made and it has been shown that such thalli possess the potentialities of only maleness or femaleness or both, it is premature to describe some species of *Lagenidium* as heterothallic or dioecious.

The so-called oogonium may be elongate, spindle-shaped, oval, ellipsoidal, almost spherical, locally paunchy, and irregular, with or without conspicuous protuberances. The antheridium is usually smaller, more elongate and cylindrical, but varies somewhat in the different species. In *L. rabenhorstii*, *L. marchalianum* and *L. enecans* it is relatively slender and cylindrical like the vegetative filaments. In *L. Cyclotellae* and *L. Oedogonii* it is usually slightly smaller than the oogonium and not particularly different in shape. In most species it forms a conspicuous perforation or conjugation tube—i.e., *L. rabenhorstii* (fig. 14), *L. marchalianum* (fig. 37), *L. enecans* (fig. 33), etc., while in the smaller species, *L. Oedogonii* and *L. Cyclotellae*, the tube is not very

evident, according to Scherffel's drawings (figs. 44, 51).

Zopf's description of fertilization in *L. rabenhorstii* is the only careful and detailed account of the process for the whole genus. After the conjugation tube has pierced the oogonium wall, the granular refractive protoplasm of the antheridium contracts into a globular mass and accumulates at the side adjacent to the oogonium (fig. 12). Shortly thereafter it begins to flow into the latter, and after approximately three hours the process is completed (figs. 13, 14). While this is going on the ooplasm begins to contract toward the tip of the conjugation tube, and at the same time the granules, bodies, and discrete elements of the protoplasm undergo visible movements. As the contraction continues the ooplasm becomes more and more coarsely granular, and by the time the antheridium is empty, the granules have coalesced into two large refringent globules (fig. 13), which later usually fuse into a single larger one (fig. 14). Fusion is then complete, and eventually the zygote becomes invested with a thick wall.

It is to be particularly noted from Zopf's account that no egg cell and periplasm are differentiated prior to fusion as in the Saprolegniales and Peronosporales, respectively. The contraction of the ooplasm during plasmogamy, however, may perhaps foreshadow this development. Cook ('35), on the other hand, described the formation of an egg cell with a definite wall prior to fusion in *L. rabenhorstii*, and in his treatment of the whole genus he frequently referred to the presence of an oosphere. His figures, however, are not very clear and convincing, and in the writer's opinion the presence of a well-differentiated egg cell remains to be shown.

In parthenogenetic species the antheridium is lacking, and the ooplasm contracts, rounds up and becomes invested with a thick wall. Germination of the oospores has been reported only in one species. In *L. rabenhorstii* this occurs within 24 hours after fertilization, according to Cook. "The wall of the oospore breaks down and a single zoospore is liberated, which . . . is almost spherical in shape, 8  $\mu$  in diameter and is provided with two large flagella" (fig. 17). He described this motile cell as a sexual zoospore in contrast to the asexual zoospores produced in sporangia. Inasmuch as nothing is known about the time and place of meiosis as well as sex determination in *Lagenidium*, Cook's use of the term sexual in this relation is obviously premature and unwarranted.

So far no cytological study of fixed and stained material has been made of the genus. Accordingly nothing is known about mitosis and the details of cytokinesis. It also remains to be seen whether the gametes are uni- or multinucleate at the time of fertilization, whether karyogamy immediately follows plasmogamy, and at what stage meiosis occurs. Such problems must first be solved before the relationship of *Lagenidium* with the higher Oomycetes becomes clear.

**L. RABENHORSTII** Zopf, 1878. Verh. Bot. Ver. Prov. Brandenburg 20: 79. 1884. Nova Acta Ksl. Leop. Carol. Deut. Akad. Nat. 47: 115. Pl. 1, figs. 1-28; pl. 2, figs. 1-9.

Thallus usually elongate, filamentous, tubular, hypha-like when young, becoming septate, thicker, 3-8  $\mu$ , vesicular and more irregular, curved, and crooked, with several short branches and protuberances; frequently attached to the host cell by the infection tube and zoospore case; confined to single cell or extending into adjacent host cells; usually slightly constricted at the septa; segments elongate, 10-20  $\mu$ , cylindrical and often irregular, sometimes breaking apart and separating; dwarf thalli usually unicellular and often *Olpidium*-like. Sporangia of the same size and shape as the thallus segments with one straight, curved or tortuous, narrow, rarely constricted exit tube, 2-3  $\mu \times$  5-20  $\mu$ , which does not project very far beyond the surface of the host; content of sporangium emerging and undergoing cleavage into zoospores outside of host; vesicle present, or doubtful. Zoospores at first bean-shaped, later becoming more pyriform and reniform, 6  $\times$  8.5  $\mu$ , isocont. Gametangia borne on the same or different thalli; oogonia terminal or intercalary, spindle- and egg-shaped, locally paunchy and irregular, or almost spherical, up to 15  $\mu$  in diameter; antheridia usually elongate and cylindrical, 5  $\times$  15  $\mu$ , or somewhat irregular; sometimes borne on a delimited branch from the oogonial cell, usually on an adjacent, or intercalary cell; developing a protuberance toward the oogonium which elongates and tapers into a perforation tube and pierces the oogonial wall; granules, bodies and discrete elements of the ooplasm undergoing slight movement, and the whole content contracting during plasmogamy; fused protoplasts contracting further and becoming invested with a wall. Oospores spherical 10-15  $\mu$ , hyaline, smooth, thick-walled with a large central refractive globule; germinating within 24 hours by giving rise directly to a large spherical 8  $\mu$ , biflagellate zoospore (?), which soon infects the host cell.

Parasitic primarily in the vegetative cells of *Spirogyra* sp., *Mougeotia* sp., and *Mesocarpus* sp. in Germany (Zopf, I.c., '79; Minden, '11); *Spirogyra* sp. in Belgium (de Wildeman, '91, '93, '95) and Roumania (Constantineanu, '01); *Oedogonium* sp. in Denmark (Petersen, '09, '10); *Spirogyra* sp. in New York and Mass., U. S. A. (Atkinson, '09; Sparrow, '32); *Oedogonium pluviosporum* and *S. orthospira* in Montana, U. S. A. (Graff, '28); *Spirogyra* sp. and *Mougeotia* sp. in Bulgaria (Valkanov, '31); *Spirogyra* sp., *S. mirabilis* and *Zygymema* sp. in Hungary (Cejp, '35; Domjan, '35). *Spirogyra* sp. in England and Wales (Cook, '32, '33, '35). The writer also has frequently found it in *Spirogyra* sp. and *Oedogonium* sp. in New York City.

Investigators are divided in their observations and opinions about the presence of a vesicular membrane around the young zoospores in this species. Zopf and Sparrow reported that zoospore cleavage and development occur within a vesicle, like in *Pythium*,

but Atkinson and Cook ('35) described the exuded protoplasmic mass as naked. In a previous paper ('32), however, Cook had reported the appearance of a thin membrane, while figure 9 and plate 1 of his 1935 contribution are very suggestive of its presence. Atkinson further described fusion of zoospores, but this appears to be an abnormal and possibly pathological behavior and apparently has no sexual significance.

Cook ('35) maintained that the content of the oogonium contracts and becomes invested with a wall before fusion, forming thus a definite oosphere or egg cell which is attached to the oogonium wall by a stalk. Zopf, on the other hand, who carefully watched the successive stages of fusion at different time intervals reported that contraction does not occur previous to but during plasmogamy and that a wall or membrane is formed only after the process has been completed. Cook's figure and description of fusion are not particularly clear, and what he described as an oosphere attached by a stalk seems to be a fertilized oospore and a conjugation tube (fig. 15).

Whether or not Cocconi's ('94) *L. papillosum* is identical with this species is uncertain. Saccardo ('88) and Minden ('11) regarded it as related, while Cook believed it to be an incompletely described specimen of *L. rabenhorstii*. According to his calculations of Cocconi's drawings, the thallus is about 5  $\mu$  in diameter, the sporangia 17  $\mu$ , zoospores 4  $\times$  6  $\mu$ , oogonia 16  $\mu$ , and the oospores 10-12  $\mu$  in diameter. The oospores, however, have a distinctly warty wall, while the zoospores are figured as pyriform with two equal anterior flagella. Cocconi's drawings of the zoospores, however, may possibly be inaccurate. It is to be noted in connection that in his early papers ('78, '79) Zopf also described the oospores of *L. rabenhorstii* as being golden in color and warty, but these observations possibly relate to *L. entophytum*.

**L. ENTOPHYTUM** (Pringsheim) Zopf, I.c., p. 154; pl. 2, figs. 10-18; pl. 3, figs. 1-3.

*Pythium entophytum* Pringsheim, 1858. Jahrb. Wiss. Bot. 1: 287, 305. Pl. 2, fig. 1.

*L. americanum* Atkinson, 1909. Bot. Gaz. 48: 331. Fig. 6.

Thallus tubular, vesicular, short, relatively thick, 4-8  $\mu$ , curved, crooked and very irregular with numerous short primary, secondary and tertiary branches or protuberances; usually constricted slightly at the cross septa; dwarf thalli continuous. Sporangia of the same size, 5  $\times$  12-15  $\mu$ , and shape as the thallus segments and dwarf thalli, exit tubes numerous, up to 20 or more, cylindrical and tortuous, 2  $\mu$  or more in diameter and of variable length, usually inflated before passing through host wall, and extending considerably beyond it; contents of sporangia emerging and forming an irregularly globular mass at the mouth of the exit tube, which may sometimes float away before cleavage is completed; vesicular membrane doubtful or absent. Zoospores bean-shaped and reniform, 4  $\times$  8  $\mu$ , isocont. Oogo-

nia locally vesicular or paunchy; antheridia lacking. Oospores numerous, parthenogenetic, formed by the contraction and encystment of the oogonium content; spherical,  $12 \mu$ , with a bright-golden, thick, smooth or warty wall, and a large central refractive globule; germination unknown.

Parasitic in the zygospores of *Spirogyra* sp. (Pringsheim, Zopf, l.c.), *Euastrum humerosum* and *Microasterias mahabaleshwarensis* var. *wallichii* (Schultz-Danzig, '23) in Germany; *Spirogyra* sp. in Belgium (de Wildeman, '91, '93, '95); *S. varians*, *S. calospora*, and *S. insignis* in New York, U. S. A. (Atkinson, l.c.), and *Spirogyra* sp. in Wales and England (Cook, '33, '35).

This species appears to have been described and figured first by Carter ('56; pl. 9, figs. 9-10) as a developmental stage of an *Astasia*-like flagellate in the zygospores of *Spirogyra*, and later by Pringsheim as a species of *Pythium*. It differs primarily from *L. rabenhorstii* by its shorter, thicker, more crooked and irregular thallus, parthenogenetic oospores, and its localization to the zygospores of the host, although de Wildeman ('95) claims that *L. rabenhorstii* also may occur rarely in zygospores of *Spirogyra*. On the other hand, *L. entophytum* is strikingly similar to *L. gracile* which inhabits the same cells, and there is a strong possibility that the two species may be identical.

Pringsheim figured and described the zoospores of his fungus as being formed exactly as in *Pythium* within a definite vesicular membrane, but Cook reported that the latter structure is missing and that the extruded mass of protoplasm is naked. Atkinson likewise failed to observe a membrane and reported that the protoplasmic mass may float away from the exit tube before cleavage. Cook further regarded the contraction and encystment of the oogonium contents as the differentiation of an egg cell or oosphere as in *L. rabenhorstii*.

In view of the fact that no other workers have found this species in other but *Spirogyra* zygospores it is perhaps questionable whether Schultz-Danzig's fungus in *Euastrum* and *Microasterias* relates to *L. entophytum*. His fungus may possibly belong to Petersen's *Myzocytium irregularare* or the unidentifed species of *Lagenidium* reported by de Wildeman ('95) in *Euastrum oblongum*. Whether Atkinson's *L. americanum* is identical to *L. entophytum* or *L. gracile*, or distinct from both is at present largely a matter of personal interpretation, but the author is inclined to agree with Minden that it relates to *L. entophytum*.

#### **L. ENECANS** Zopf, l.c., p. 154. Scherffel, 1925. Arch. Protistk. 52: 20. Pl. 2, figs. 60-69.

Thallus sparingly branched with short plump, finger-like branches,  $6-12 \mu \times 37-156 \mu$ ; attached to host cell by infection tube; apparently continuous, transformed completely into a zoosporangium at maturity. Exit tube cylindrical,  $3-6 \mu \times 9-36 \mu$ , extending only slightly beyond the surface of the host; thickened and inflated at base to form a "spreading apparatus" which enables it to pass be-

tween the valves of the host cell. Zoospores egg- and kidney-shaped, elongate with a ventral groove,  $5.7 \mu \times 8-12.5 \mu$ ; secondary swarmers heterocont with the short flagellum directed forward; vesicular membrane not clearly evident. Oospores spherical,  $18 \mu$ , broadly oval,  $15-22 \mu \times 20-24 \mu$ , and irregular with a smooth thick wall, large central refractive globule, and finely granular protoplasm; germination unknown.

Parasitic in *Stauroneis phoenocenteron*, *Coccinea lanceolatum* and *Pinnularia* sp., in Germany (Zopf, l.c.); various diatoms in Belgium (de Wildeman, '93); *Gomphonema constrictum*, *Cymbella cymbiformis* var. *parva*, *C. gastrooides*, *Cymatopleura solea*, *Stauroneis phoenocenteron*, *Amphora ovalis*, and *Cocconeina lanceolatum* in Hungary (Scherffel, '02, '25); *Navicula cuspidata* var. *ambigua* and *Stauroneis phoenocenteron* in China (Skvortzow, '31).

Inasmuch as Zopf and none of the subsequent workers except possibly de Wildeman had figured this species, Scherffel was not certain that the form which he found relates to *L. enecans*, although he described it as such.

#### **L. PYGMAEUM** Zopf, 1887. Abh. Naturf. Ges. Halle 17: 97. Pl. 1, figs. 21-39; pl. 2, figs. 1-12.

Thalli usually solitary, sometimes 2-4 in a host cell, oval, spherical, ellipsoidal and *Olpidium*-like, or elongate, irregular and lobed with one or several short branches or protuberances; often completely filling the host cell; unicellular or dividing into an antheridium and oogonium at maturity. Exit tubes short, thick, tapering, and rarely branched, usually extending but a short distance beyond the host cell. Zoospores bean-shaped,  $5 \times 8 \mu$ , tapering at the anterior and more rounded at the posterior end with a ventral groove and several small refractive granules; delimited in the sporangium, emerging in succession, and completing their development in an extramatrical vesicle; swarming in the latter and freed by its rupture; intermittently amoeboid. Oogonia oval, paunchy and slightly irregular with protuberances; antheridia smaller with none or fewer and less conspicuous protuberances; conjugation canal usually well developed. Oospores predominantly spherical and oval, sometimes ellipsoidal and slightly elongate,  $18-29 \mu$  in diameter, hyaline, smooth, and thick-walled, with a large refractive globule; germination unknown.

Parasitic in pollen grains of *P. sylvestris*, *P. austriaca*, *P. laricio*, *P. pallasiana*, *Pinn* sp., and *Cosmarium pyramidatum* in Germany (Zopf, l.c.; Schultz-Danzig, '23), pollen grains in Switzerland (Maurizio, '95) and conifer pollen in Belgium (de Wildeman, '95) and Denmark (Petersen, '09, '10).

The author ('41) collected this species in pollen of *P. austriaca* in New York City and succeeded in transferring it to pollen of *P. sylvestris*, *P. banksiana*, *P. densiflora*, *P. thunbergii*, *P. strobus*, *P. austriaca* var. *nigra* and hemlock. Attempts were also made to infect living and killed cells of *Nitella flexilis*, *Chara coronata*, *Cladophora glomerata*,

*Pithophora* sp., *Stigeoclonium tenue*, *Ulothrix zonata*, *Oedogonium* sp., *Spirogyra* sp., *S. crassa*, *Mougeotia* sp., and *Hydrodictyon reticulatum* without success. These results cast doubt on Schultz-Danzig's report of the occurrence of this species in *Cosmarium*. He based his claim on the presence of an irregular, lobed, sac-like thallus with an exit tube which is rarely branched, and the presence in the same culture of pollen grains infested with *L. pygmaeum*. It is not improbable that his fungus relates to dwarf thalli of *Myzocystium* or another species of *Lagenidium*. Zopf's report that the zoospores are 16 to 18  $\mu$  long is obviously incorrect. The present writer has observed their formation and activity numerous times and found them to be approximately  $5 \times 8 \mu$  in size and bean-shaped with a ventral groove.

Thalli of this species may look strikingly like those of *Olpodium*, and unless zoospore emergence is observed they may readily be mistaken for this ephytid. Fischer believed that the intramatrical resting spores of *R. pollinis* noted by Cornu ('72, p. 121) relate to *L. pygmaeum* also. Atkinson ('09) believed that the zoospores of *L. pygmaeum* species are diploid—the emergence of the incompletely developed zoospore segments representing the initial motile stage.

Whether Serbinow's ('99) *Olpodium ramosum* relates to this species or belongs at all in the genus *Lagenidium* is very doubtful. Mention is nevertheless made of it here because it occurs in pollen grains of *Pinus sylvestris* in Russia and is reported to form oospores. However, the zoospores are fully formed in the zoosporangium, possess a single posterior flagellum, and swim directly away after emerging from the branched exit tubes. In sexual reproduction two thalli, apparently of unequal size, fuse within pollen grains and become invested with a thick wall. This type of fusion is suggestive of that which occurs in *Olpidiopsis*, but the presence of posteriorly uniflagellate zoospores excludes *O. ramosum* from this genus as well as from *Lagenidium*.

**L. GRACILE** Zopf, I.c., p. 158. Cook, 1932, New Phytol. 31: 140. Figs. 32-38. 1935. Arch. Protistk. 86: 88. Pl. 3, figs. 26-32.

Thallus very similar to that of *L. entophytum* but usually narrower, 4.5  $\mu$ , and less irregularly branched, sometimes penetrating adjacent host cells. Sporangia less irregular, tubular, cylindrical, 4.5  $\mu$  in diameter, and occasionally almost spherical with a narrow unconstricted exit tube of variable length, which may become inflated before passing through the zygospore and gametangium wall of the host; extending for varying distances beyond. Zoospores bean-shaped,  $4 \times 7.5 \mu$ , formed in an extramatrical vesicle (?); vesicular membrane doubtful. Oogonia intercalary, rarely terminal, oval, globular, paunchy; antheridia lacking. Oospores few or numerous, parthenogenetic, formed as in *L. entophytum*, spherical, 13-14  $\mu$ , with a thick smooth wall; germination unknown.

Parasitic in the zygospores of *Spirogyra* sp. in Germany (Zopf, I.c.); *S. grevilleana* in Belgium (de Wildeman, '95), and *Spirogyra* sp. in England (Cook, I.c.).

From the above description, the validity of this species seems very questionable. The slight differences in diameter, irregularity of branching, length and diameter of exit tubes, etc., noted by Zopf and subsequent workers are not sufficient to distinguish it sharply from *L. entophytum*, and inasmuch as both are parthenogenetic and inhabit the zygospores of *Spirogyra*, the author is strongly of the opinion that they are identical. Zopf's claim that the oospores differ by being smooth and not bright golden in color does not seem particularly significant, since such oospores have been reported in *L. entophytum* also.

**L. ZOPFII** de Wildeman, 1891. Bull. Soc. Belge Micro. 16: 139. Petersen, 1909. Bot. Tidskr. 9: 401. Fig. XV1b.

Thallus irregular, branched, septate; consisting of elongate, cylindrical and vesicular segments, and extending through 3-4 host cells. Sporangia and zoospores unknown. Oogonia vesicular and paunchy; oospores 14  $\mu$  in diameter with an irregular warty wall; content refractive, large globule lacking; germination unknown.

Parasitic in *Oedogonium* sp. in Belgimm (de Wildeman, I.c.) and Jutland (Petersen, '09, '10).

This species has been reported but twice, and Petersen's single figure of it is the only one extant, as far as the writer is aware. De Wildeman ('93, p. 11) and Minden ('11) believed it may possibly be identical to *L. syncytiorum* described below, and Cook ('35) listed it as a synonym of the latter species. However, if the two are identical, *L. syncytiorum* should be the synonym, since *L. zopfii* has priority. While the author is inclined to agree with the view at present that they may be identical, both species are too incompletely known to warrant definite conclusions. For this reason they are herewith treated as distinct species for the time being. According to de Wildeman, the thallus is similar to that of *L. rabenhorstii*, but Petersen described it as narrower and less branched. The oospores, on the other hand, resemble those of *L. entophytum*.

**L. SYNCYTIORUM** Klebahn, 1892. Jahrb. Wiss. Bot. 24: 263. Pl. 3, figs. 22-24.

Thallus at first straight, 3-5  $\mu$ , irregular, curved, beady, filamentous and continuous; later becoming septate and more irregular with numerous protuberances; extending through several incompletely divided host cells. Thallus segments and sporangia spherical, oval, ellipsoidal, 8-10  $\mu$  in diameter, spindle-shaped, elongate, curved and somewhat irregular with a single short exit tube which does not project very far beyond the host cell. Zoospores, oogonia, antheridia and oospores unknown.

Parasitic in *Oedogonium boscii* in Germany (Klebahn, I.c.) and *Oedogonium* sp. in Belgium (de Wildeman, '95).

This species has been reported but twice, and is so incompletely known that it is impossible to determine whether or not it is identical to *L. zoppii*. De Wildeman, however, was inclined to regard the fungus which he found at Nancy as distinct from *L. zoppii* and possibly related or identical to Sorokin's *Aphanistis pellucidia*. It is to be noted here, however, that the zoospores of the latter species are uniflagellate, according to Sorokin.

According to Klebahn, *L. syncytiorum* has but little deleterious effect on the host cells at first. Nuclear division may proceed normally for a time, but cell division is not completed. As a result, infected cells may be multinucleate with incompletely formed cross walls, and 2-4 times their normal length. In these respects the effects are very similar to those caused by *Plasmophagus* in the same host (de Wildeman, '95, p. 220). De Wildeman, on the other hand, failed to observe the effects described by Klebahn, and found that the thallus may be confined to a single cell the content of which it soon destroys. According to Klebahn, all host nuclei in infected cells are not similar in size and shape. Some may be large while others are quite small, suggesting perhaps a previous disturbance in chromosome distribution. As the parasite matures the effects on the host become more pronounced. The plastids, nuclei, and the remainder of the protoplasm are gradually killed and largely absorbed.

The irregular thalli of this species resemble somewhat those of *L. ellipticum*, while those in which the segments are arranged like a string of beads look similar to thalli of *Myzocytium megastomum*.

**L. ELLIPTICUM** de Wildeman, 1893a. Ann. Soc. Belge Micro. 17: 5. Pl. 1, figs. 1-11. 1893b. Jour. Roy. Micro. Soc. 1893: 765.

Thallus thick, deeply lobed and irregular with numerous blunt protuberances, rarely becoming filamentous, non-septate and continuous with one or more short exit tubes which project only slightly beyond the surface of the host. Zoospores, oogonia and antheridia unknown. Oospores elliptical, 10-14  $\times$  20-30  $\mu$ , with a thick irregularly warty wall, and a granular refractive content; germination unknown.

Parasitic in rhizoids of mosses in Belgium.

De Wildeman was not certain about the relationship of this species to *Lagenidium*, and in view of the fact that no zoospores, oogonia and antheridia have been observed it is herewith presented as very doubtful. The oospores are usually numerous, but de Wildeman did not determine whether or not they are parthenogenetic.

**L. CLOSTERII** de Wildeman, 1893b. Ann. Soc. Belge Micro. 17: 42. Pl. 6, figs. 1-3.

Thallus mycelium-like, consisting of long, straight, curved, twisted, branched, cylindrical filaments of more or less uniform, 1.8-2.8  $\mu$ , diameter; occasionally swollen, vesicular, and irregular, usually unconstricted; becoming septate at maturity; segments transformed into sporangia or gametangia.

Sporangia elongate and cylindrical; exit tubes greatly inflated, globular and appressorium-like inside of host wall and extending a short distance or 20-30  $\mu$  beyond its surface. Zoospores bean-shaped, 3.8  $\mu$   $\times$  5.6-6.3  $\mu$ ; formed in an extramatrical vesicle. Oogonia inflated and broadly spindle-shaped, antheridia less so. Oospores spherical 10-15  $\mu$ , with a double-layered wall, exospore warty, verrucose or knobbed; germination unknown.

Parasitic in *Closterium striolatum* in Belgium (de Wildeman, l.c.); *Closterium* sp., in Denmark (Petersen, '09, '10), Czechoslovakia (Cejp, '33, '35) and North Carolina, U. S. A. (Couch, '35).

The warty or verrucose oospores of this species are very similar to those of *L. entophysum* and *L. zoppii*, but differ from those of these two species by the possession of a large central refractive globule, according to de Wildeman. Minden regarded this species as doubtful, but Conch thought it may be valid. The latter worker pointed out that it may readily be mistaken for a species of *Pythium* because of its fine, filamentous thallus, but the large refractive granules in the cytoplasm, however, distinguish it rather clearly.

**L. INTERMEDIUM** de Wildeman, 1895. Ann. Soc. Belge Micro. 19: 96. Pl. 4, figs. 10-13.

Thallus irregular, rather thick, frequently branched and sparingly septate. Sporangia tubular, elongate and cylindrical with a single exit tube which may be rarely inflated inside of the host wall, constricted as it passes through, and extends a short or long distance beyond the surface of the host. Zoospores, oogonia and antheridia unknown. Oospores globular, smooth and thick-walled; germination unknown.

Parasitic in *Closterium chrenbergii* in Belgium (de Wildeman, l.c.); *Closterium* sp., and *Pleurotaenium trabecula* in Bohemia (Cejp, '35).

This species has been observed but twice and is imperfectly known. Cejp did not add anything of significance to the original description of de Wildeman. By its elongate and cylindrical segments this species resembles *L. rabenhorstii*, and according to de Wildeman it stands intermediate between the latter species and *L. entophysum*.

De Wildeman (l.c., p. 75; pl. 2, fig. 22) also figured an extensively lobed parasite in *Euastrum oblongum* which he believed relates to *Lagenidium*. He did not, however, observe the zoospores and oospores, and hence it is difficult to determine the identity of the species. He, nonetheless, believed it may be the same fungus which Reinsch ('78, pl. 17, fig. 5) figured in *E. oblongum*. Cornu ('77), however, believed Reinsch's fungus relates to *Myzocytium lineare*.

**L. REDUCTUM** (de Wildeman) nov. comb.

*Lagenidiopsis reducta* de Wildeman, 1896. Ann. Soc. Belge Micro. 20: 109. Pls. 6-7.

Thallus filamentous, elongate, tubular, cylindrical, straight, curved and undulate, slightly inflated

at the ends, rarely branched, continuous and unicellular with the short infection tube and zoospore case persistent. Sporangia and zoospores unknown. Oogonia globular, oval and almost spherical; beginning as a terminal or intercalary swelling and with further growth becoming somewhat lateral in position but continuous with the main axis. Antheridia oval, clavate, and cone-shaped; borne on the oogonium and delimited from the latter by a cross wall; usually disintegrating and disappearing after fertilization; conjugation tube usually well-developed and conspicuous. Oospores single, rarely double, spherical, oval, ellipsoid and egg-shaped, 13–19  $\mu$  in diameter, with a thick rough or warty wall; content granular with one or more refractive globules; germination unknown.

Parasitic in the oogonia of *Chara* in Switzerland.

De Wildeman created the genus *Lagenidiopsis* as an intermediate group between the Lagenidiales and Peronosporales, primarily because the thallus is filamentous and unicellular. These characters, however, are no longer of significance in this case, since similar thalli have subsequently been found to be characteristic of certain species of *Lagenidium* also. Furthermore, the method of sexual reproduction in *Lagenidiopsis* is typical of that in the former genus, and on these grounds it seems logical to merge the two genera. Their identity or difference, however, cannot be definitely settled until the sporangia and zoospores of *Lagenidiopsis* have been found.

**L. MARCHALIANUM** de Wildeman, 1897. Ann. Soc. Belge Micro. 21: 8, Pl. 1, figs. 1–9.

Thallus filamentous, cylindrical, 2.2–6.7  $\mu$  in diameter, sometimes irregularly swollen, slightly or not at all constricted; occasionally confined to a single cell, but usually extending through six or seven host cells; enlarged up to 7  $\mu$  in diameter before entering the cross septa of the host and constricted to 1  $\mu$  as it passes through. Sporangia cylindrical, elongate, 30–60  $\mu$ , narrowly spindle-shaped with a delicate, 1.5–2  $\mu$  thick, exit tube which extends 4–5  $\mu$  beyond the host cell. Zoospores unknown. Oogonia spherical, 20  $\mu$ , intercalary, rarely terminal; antheridia adjacent to oogonia on the same filaments, or arising as a branch from an adjacent filament. Oospores spherical, 8–14  $\mu$ , hyaline, smooth, thick-walled, rarely parthenogenetic; germination unknown.

Parasitic in *Oedogonium* sp. in Belgium (de Wildeman, l.c.) and Virginia, U. S. A. (Couch, '35).

**L. OEDOGONII** Scherffel, 1902. Hedwigia 41: (105). 1925. Arch. Protistk. 52: 109, Pl. 5, figs. 209–219.

Thallus usually single, rarely two or more in a cell, ovoid, vesicular, 20–25  $\mu \times$  35–52  $\mu$ , irregular, lobed, with blunt protuberances, rarely filamentous, filaments when present several hundred microns in length and coiled; non-septate and continuous with one exit tube which may end almost flush with the surface of the host cell or extend considerably beyond it. Zoospores mono- or diplanetie; fully formed

in the sporangium or delimited in an extramatrical vesicle with an indistinct membrane; in the former case emerging singly and encysting in a group at the mouth of the exit tube, later germinating and leaving the 4–6.6  $\mu$  in diameter, cysts behind as in *Achlya*; secondary zoospores or swarmers pointed at the anterior and round at the posterior end with a ventral groove, heterocont with the short flagellum directed forward; forming an appressorium on the host wall in germination. Oospores globular, spherical, 12–14  $\mu$ , with a 2  $\mu$  thick, hyaline, smooth wall and containing coarsely granular protoplasm and a large eccentric globule; germination unknown.

Parasitic in *Oedogonium* sp. in Hungary (Scherffel, l.c.) and Missouri, U. S. A. (Couch, '35).

This is a significant species because its zoospores exhibit several characteristics common to *Pythium* and *Achlya*. The zoospores may be formed extramatrically in a vesicle as in *Pythium*, or within the sporangium and then emerge and encyst at the mouth of the exit tube as in *Achlya*. It is to be noted in this connection that the zoospores of *Olpidiopsis Oedogoniorum* have the same characteristics, while its resting spores and their method of formation are also strikingly similar to the oospores of *L. Oedogonii*. Scherffel accordingly pointed out that *O. Oedogoniorum* has much in common with *Lagenidium*, and was of the opinion that it may relate to the latter genus. From his drawings and descriptions of the thalli one might believe that the two species are closely related or even identical, but the elongate thalli of *L. Oedogonii* which Couch figured are distinctly unlike those of *Olpidiopsis*. It is nevertheless obvious that further study and comparison is very essential to an understanding of the two species.

In this species Scherffel found segments of the thallus or possibly of sporangia the contents of which had contracted, become septate, and thick-walled. He regarded these resting structures as comparable with the gemmae of the Saprolegniaceae, but it is doubtful that they are of any particular morphological or phylogenetic significance.

**L. SACCULOIDES** Serbinow, 1924. La Defense des Plantes 1: 85.

Thallus short, unicellular, sac-like with lobes or short branches, or narrowly elongate, 3.5–7.6  $\mu$  in diameter, with occasional septa. Zoospores apparently completing their development in an extramatrical vesicle; spherical, 3.5  $\mu$ , in fixed and stained preparations; position and relative lengths of flagella and presence of diplanetism unknown. Sexual reproduction isogamous; contents of two adjacent cells flowing together and forming a zygospore (?) in the space between them. Zygospores hyaline, spherical, 13.3  $\mu$ , oval, elongate, 7.6  $\mu \times$  15.2  $\mu$ , with a sculptured outer and a smooth inner wall; containing a large refractive globule; germination unknown.

Parasitic and saprophytic in *Closterium ralfsii* var. *hybridum* in the Menzelinsk district of the Ufimsk province in Russia.

Serbinow's study of this species relates to material collected in 1913 and fixed in glycerine jelly. Consequently the method of zoospore formation, motility and behavior of the zoospores, relative lengths and position of the flagella, as well as the successive stages of sexual reproduction were not observed. Whether or not it belongs in *Lagenidium* is questionable. Because of the lack of or reduced branching of the thallus Serbinow regarded it as intermediate between this genus and *Myzocytium*. Its method of sexual reproduction, however, seems strikingly similar to that described by Dangeard for *Resticularia nodosa*. Until more is known about *L. sacculoides*, its relationship to the above-mentioned genera will remain doubtful. Serbinow did not illustrate this species, as far as the present writer is aware. Its effect on the host is quite marked. It kills the desmid cells very quickly and soon destroys their contents, but it is not an obligate parasite, according to Serbinow. It may also attack dead and partly empty cells.

**L. CYCLOTELLAE** Scherffel, l.c., p. 18. Pl. 2, figs. 49-59.

Thallus small, sac-like, and continuous, attached to the extramatrical persistent zoospore case by the germ or infection tube; transformed completely into a single sporangium at maturity, with a short, 3  $\mu$  wide exit tube. Zoospores fully formed in the sporangium; emerging singly and swimming directly away; oval, egg-shaped, 3.5  $\mu$   $\times$  6  $\mu$ , slightly concave with a refractive mass near the posterior end; flagella attached slightly below the apex. Oospores globose, 10  $\mu$ , broadly oval, 8-10  $\mu$   $\times$  10-12  $\mu$ , angular and somewhat irregular, hyaline, smooth, thick-walled; containing a large refractive globule, granular protoplasm, and a lateral spot; germination unknown.

Parasitic in *Cyclotella kutzningiana* in Hungary.

The manner of zoospore formation and emergence in this species are very similar to those of *L. pygmaeum* and *L. oophilum*. In shape and appearance, however, the zoospores are more like those of *Ectrogella bacillariacearum*, according to Scherffel. He did not observe diplanetism but believed that it occurs. Scherffel regarded this species as a connecting link between *Ectrogella* and the *Lagenidiaceae* (Aneylistaceae).

**L. BRACHYSTOMUM** Scherffel, l.c., p. 21. Pl. 2, figs. 70-85.

Thallus elongate, 4-7.5  $\mu$   $\times$  150-250  $\mu$ , usually unbranched or with short side branches and protuberances; continuous, and transformed completely into a single sporangium at maturity with one or rarely two very short, tapering cone-shaped exit tubes, the wall of which is greatly thickened at the base to form a spreading apparatus. Exit tubes forcing the valves of host cell apart, boring through the wall. Zoospores kidney-shaped with a ventral groove, 4  $\times$  6-8  $\mu$ , formed in an extramatrical ves-

icle as in *Pythium*. Oospores formed parthenogenetically or by sexual fusion, globose, broadly-oval, 6-10  $\mu$   $\times$  11-24  $\mu$ , hyaline, smooth, thick-walled with one or two large refractive globules; germination unknown.

Parasitic in *Synedra ulna*, *Cymbella cymbiformis* var. *parva*, *Gomphonema constrictum* and *Nitzschia linearis* in Hungary (Scherffel, l.c.) and *Synedra* sp. in North Carolina, U. S. A. (Couch, '35).

This species differs from *L. enecans*, according to Scherffel, by its unbranched thallus, thin wall, short, cone-shaped exit tubes, and the fact that it parasitizes small diatoms. As he pointed out, however, it may also occur in *Cymbella cymbiformis* var. *parva*, which is also often parasitized by *L. enecans*. Many of the structural differences which Scherffel described above may possibly be due to the smaller hosts in which this species lives and do not relate to fundamental specific characters. Until extensive cross inoculation experiments have been made, the validity of *L. brachystomum* must be regarded with question.

Scherffel (l.c., p. 23; pl. 2, fig. 86) further described a species of *Lagenidium* with a long sparingly branched, multiseptate thallus in *Pinnularia* sp., which bears some resemblance to *L. rabenhorstii*. The exit tubes are fairly long and cylindrical and extend for some distance beyond the surface of the host cell. No zoospores nor their method of formation were observed. The oospores are solitary, globose and appear to have arisen by sexual fusion. Scherffel was doubtful about whether this species is homo- or heterothallic, but he felt certain that it is not identical to *L. enecans*.

**L. GIGANTEUM** Couch, 1935. Mycologia 27: 376. Figs. 1-19.

Thallus coarse, extensive and mycelioid, branched, constricted or unconstricted; extramatrical branches somewhat fine and delicate. Sporangia elongate and cylindrical, 6-40  $\mu$   $\times$  50-300  $\mu$ , with a single, long 6-10  $\mu$   $\times$  50-300  $\mu$ , exit tube; content emerging through the tube to form one or several globular, naked and undifferentiated masses, which undergo cleavage into zoospores. Zoospores slightly oval, 8-9  $\mu$   $\times$  9-10  $\mu$ , with a ventral groove in which two equal flagella are attached; freed by the rupture or deliquescence of the vesicular membrane. Monoplanetic and rather sluggish. Sexual reproduction unknown.

Weakly parasitic on mosquito larvae, copepods and *Daphne* in Virginia, U. S. A. (Couch, l.c.; Matthews, '35) and mosquito in North Carolina, U. S. A. (Couch, l.c.).

Couch succeeded in growing this species on various synthetic culture media and isolated what he believed to be a mutant of the original strain. His is the first report of the culture of a species of *Lagenidium* apart from its host tissues. Since sexual reproduction has so far not been observed, Couch was somewhat in doubt about whether this species re-

lates to *Lagenidium*. It differs from any of the other species in being a weak facultative parasite and having an extensively branched filamentous, mycelioid thallus.

Another unidentified species has been recorded by Couch ('35, p. 385, figs. 32-34) in *Oedogonium* which he took to be *L. brachystomum*. The thallus is ovoid and slightly irregular,  $7-10 \mu \times 15-20 \mu$ . The zoospores are formed in an extramatrical vesicle, and after swimming about for a short while, encyst. Within one to three hours they emerge and become motile again. In rare cases encysted spores which have germinated with a tube emerge, leaving the germ tube and cyst behind. No stages of sexual reproduction nor oospores have been observed.\*

**L. OOPHILUM** Sparrow, 1939. Mycologia 31: 531. Figs. 1-14.

*Lagena oophilum* Sparrow, l.c.

Thallus solitary or several in a host cell, irregularly saccate, ellipsoidal, broadly lobed or non-lobed; converted holocarpically into a thin-walled hyaline zoosporangium,  $12-25 \mu$  wide by  $20-40 \mu$  long, with a short sessile or slightly prolonged exit papilla,  $4-5 \mu$  in diameter. Zoospores grape seed-shaped, laterally biflagellate, isocont,  $6 \times 8 \mu$ , emerging individually and maturing in a globular group at the exit orifice, vesicle doubtful or unknown; cystospores  $5-6 \mu$  in diameter. Sexual reproduction unknown.

\* Since this volume went to press another species of *Lagenidium* has been reported and described by Couch in the eggs and newly-hatched individuals of the common blue crab in Virginia. It is the only known marine species of this genus and is characterized by a coarse, branched, sparingly septate mycelium, a persistent vesicle, and asexual resting spores. Its mycelium is very similar to that of *L. giganteum*, and Couch believes that the two species are closely related. Unlike the latter species, however, it will not grow on nutrient agar made with fresh water. Its economic significance as a parasite is not known, but it kills the infected eggs and young individuals. Parasitized eggs of the host can be distinguished from normal ones by their smaller size and greater opacity.

**L. CALLINECTES** Couch, 1942. Jour. Elisha Mitchell Sci. Soc. 58: 158. Pls. 18, 19.

Thallus predominantly intramatrical, mycelioid, coarse, irregularly branched, sparingly septate, thin-walled,  $5.4-12.6 \mu$  in diameter; each segment becoming a sporangium. Extramatrical emergence papilla of sporangium tubular,  $11-29 \mu \times 25-70 \mu$ ; protoplasm emerging as an irregular, subspherical or spherical mass, up to  $100 \mu$  in diameter, and becoming enveloped by a persistent, thick, gelatinous envelope or vesicular membrane; cleaving into zoospores as in *Pythium*. Zoospores swarming in persistent vesicle and later liberated by its rupture; tapering at the anterior and rounded at the posterior end,  $9.6 \times 12.6 \mu$ , with a diagonal groove; containing several oil globules; isocont (?), flagella inserted laterally (?) in groove and extending in opposite directions in swimming; zoospores coming to rest and encysting, cystospores oblong or subspherical,  $10-11.3 \mu$ ; monoplastic. Resting spores asexual, spherical, subspherical or oval,  $18-30 \mu$ , with a  $3 \mu$  thick wall; containing pale whitish protoplasm and an excentric mass of oil globules; germination unknown.

Parasitic in the eggs and newly-hatched individuals of *Callinectes sapidus* in Virginia, U. S. A.

Parasitic in rotifer eggs and embryos, Huron River, Ann Arbor, Michigan.

Inasmuch as its sexual reproduction is unknown, the validity of this species is questionable. Sparrow was doubtful about its identity, as is indicated by the two names proposed above. He stressed the similarity of its unicellular vegetative thallus to those of *Myzocytium zoophthorum*, *L. Oedogonii*, and *Lagena radicicola*, particularly when the latter's thalli are reduced. His suggestion of including this species in *Lagena* because of its unicellular thallus is not of much merit in light of Truscott's ('33) earlier observations that the thallus of *L. radicicola* may be greatly elongate, tubular and branched. Obviously size and shape of thallus in this group of fungi are not always fundamental diagnostic characters. It may be noted further that *L. oophilum* also resembles *L. pygmaeum* in zoospore size as well as in shape and size of thallus (Karling, '41). Cross inoculation experiments involving the respective hosts of these two species may possibly show that they are identical. Sparrow made no attempt to grow his species on any hosts but rotifers.

The irregular, stout,  $3-8 \mu$  in diameter, branched thallus which Sparrow ('36, pl. 17, figs. 13-15) previously found in cysts of *Euglena* resembles that of *Lagenidium* and may possibly relate to this genus. Elliptical,  $10 \times 13 \mu$ , thick-walled resting spores were also observed in association with empty thalli. Sparrow also believed that the irregular, immature thallus (pl. 19, fig. 16a) which he found in a dead nematode may belong in this genus.

In this connection it may be noted that Deckenbach ('03) found a marine species of *Lagenidium* at Balaklawa which parasitizes *Chaetomorpha aerea*. However, he did not describe or diagnose it and merely stated that it differs from the then known freshwater species by its large size.

Two additional species of *Lagenidium* (?) were reported by Scherffel ('26, p. 246) in *Oedogonium frankliniana* and *Penium digitus* but he did not identify them.

## MYZOCYTIUM

Schenk, 1858. Über das Vorkommen Contraciliärer Zellen im Pflanzenreich, Wurzburg, p. 10.

*Bericum* Sorokin, 1883. Arch. Bot. Nord France 2: 43.

(PLATES 21, 22)

Thallus intramatrical, holocarpic; unbranched, usually elongate, cylindrical and continuous when young, later becoming septate and constricted; occasionally reduced to one or two segments and becoming *Olpidium*-like. Zoosporangia formed directly from the segments of the thallus, oval, ellipsoid, spherical, elongate and cylindrical, hyaline

and smooth with one or two exit tubes of varying length which may project slightly or considerably beyond the surface of the host cell. Zoospores bean-shaped with two flagella inserted laterally in a slight depression, and several small refractive granules; partially formed in the sporangium, emerging in succession, and completing their development in an extramatrical vesicle, or developing completely on the outside within a vesicle, and eventually rupturing the vesicular membrane. Gametangia formed in the same manner as, and often intermingled with, the sporangia; antheridia usually of the same size and shape as and alternating with the oogonia; no differentiation of egg cell, or oosphere and epiplasm prior to fusion; content of antheridia passing through a pore or small conjugation tube into the oogonium; fused protoplasts contracting to form a spherical or globose oospore with a thin endospore, a thick smooth, stellate or sculptured exospore; containing one to several refractive globules; germinating by becoming transformed directly into a zoosporangium.

*Myzocytium* includes at present five species, two of which are doubtful. These species are parasites of desmids, green filamentous, fresh-water algae, nematodes and rotifers in Asia, Europe and North America. The development of the thallus is comparatively simple. As is shown in figures 3 and 4, the zoospore becomes attached to the host, develops a germ tube which penetrates the host wall and enters the lumen of the cell. The content of the spore passes into the tip of the tube, which then elongates, increases in size, and eventually becomes the young thallus. It soon begins to absorb food from the host protoplasm and elongates further into a thick, straight, curved, irregular or lobed structure which may often extend the full length of the host cell and even into an adjacent one. In the meantime, the zoospore case and part of the germ tube disappear. At this stage the host protoplasm is usually clumped around the thallus and often obscures it, particularly in *M. proliferum* (figs. 6, 7, 9, 16). By the time the thallus is mature most of the protoplasm has been absorbed, so that the host cell is almost empty, except for the parasite and a few extraneous granules.

In the early developmental stages the thallus is continuous, but as it matures it becomes septate and consists then of a linear series of cells. According to Dangeard ('06) it is multinucleate from the early stages on. By further expansion of the individual segments, it usually becomes constricted at the septa, so that the thallus often appears as a series of beads connected by short refractive isthmuses (figs. 5, 19, 37). The segments may occasionally break apart at the septa, giving rise thus to a number of free cells within the host. The zoosporangia are developed directly from the segments of the thallus. In the early stages they usually possess several small vacuoles, but these generally fuse to form a large central one as the exit tubes develop. In addition, the protoplasm includes a large number of

conspicuous refractive granules, which apparently break up into smaller and smaller fragments as sporogenesis approaches, with the result that the protoplasm loses some of its refractive appearance and becomes more greyish-granular.

There is considerable disagreement among students of this genus as to where the zoospores are delimited. Many of the early investigators described the protoplasm as emerging through the exit tube and forming an extramatrical vesicle as in *Pythium*, which then underwent cleavage into swarm-spore initials (figs. 10-17). With further development and maturity these become actively motile in the vesicle and are freed eventually by the rupture or deliquescence of the vesicular membrane. The more recent workers, however, maintained that zoospore rudiments are first delimited in the sporangium, pass out singly in succession, and complete their development at the mouth of the exit tube. That they may even be completely formed in the sporangium is supported by the fact that zoospores may frequently be seen swarming inside. According to these latter investigators a vesicular membrane is visible only during the initial stages of zoospore emission (figs. 28, 44, 45). The process of sporogenesis doubtless varies to some degree in the different species, but it is probable that the early workers were somewhat in-

#### PLATE 21

##### *Myzocytium proliferum*

(Figs. 1, 2, 5-19 after Zopf, '84)

Figs. 1, 2. Laterally biflagellate heterocont zoospores.

Figs. 3, 4. Infection stages.

Fig. 5. Young thallus in *Spirogyra* cell; A, unicellular, B, bicellular, and C, four-celled thallus.

Figs. 6-9. Successive developmental stages of a tricellular thallus; fusiform antheridium in center, sporangium on right, and oogonium on left.

Figs. 10-15. Emergence of protoplasm from sporangium, and stages in cleavage and maturation of zoospores within a vesicle.

Fig. 16. A six-celled thallus, all segments of which developed into sporangia.

Fig. 17. Reduced *Olpodium*-like thallus with zoospores in a vesicle.

Fig. 18. Reduced thallus consisting of an antheridium, oogonium, and oospore.

Fig. 19. Elongate thallus with oospores.

##### *M. vermiculatum*

(Figs. 20-24, 27-35 after Dangeard, '06; figs. 25, 26 after Zopf, '84.)

Fig. 20. Laterally biflagellate heterocont zoospores.

Figs. 21, 22. Early germination stages.

Fig. 23. Elongate irregular germination zoospore on nematode.

Fig. 24. Infection.

Fig. 25. Unicellular thallus from nematode.

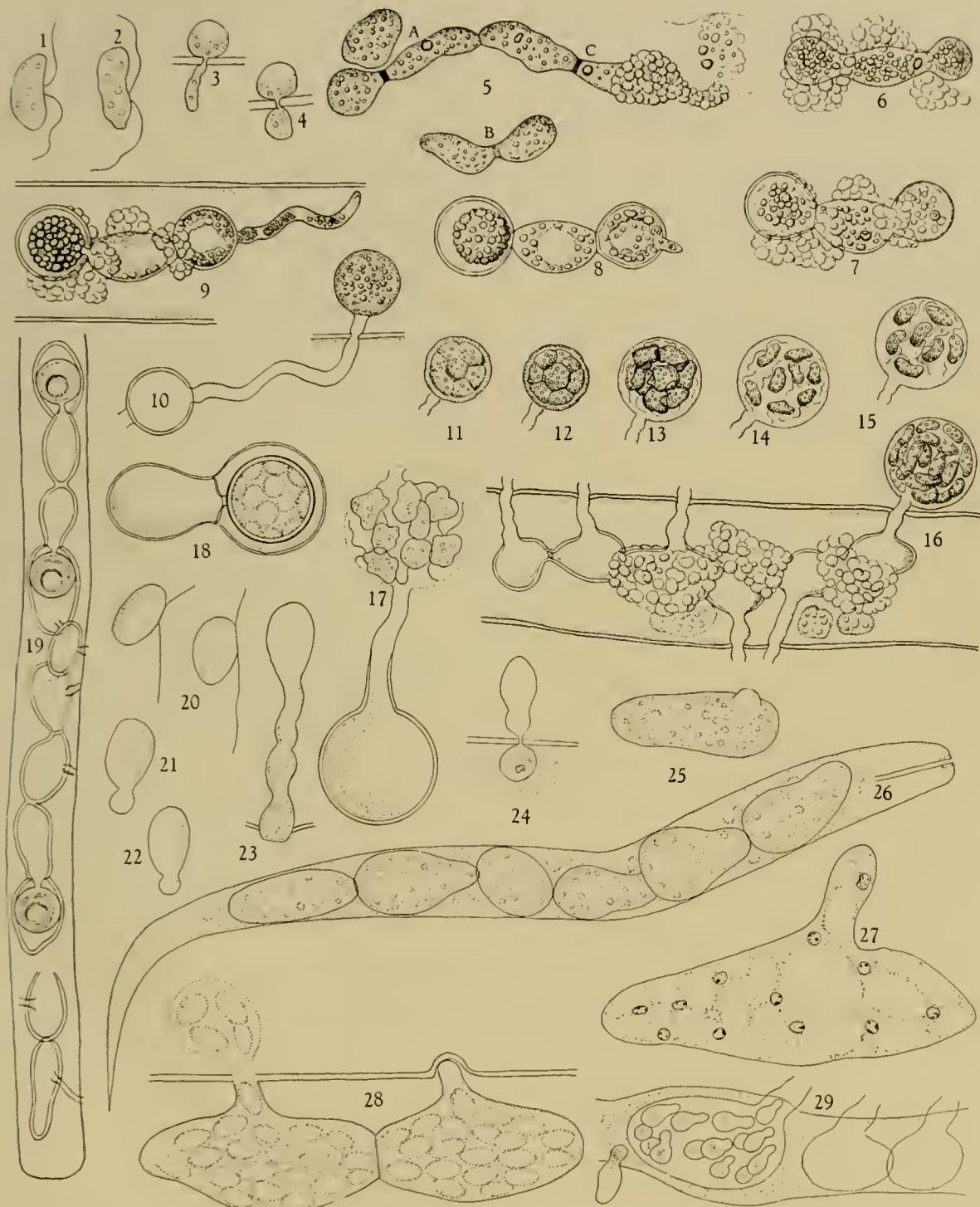
Fig. 26. Nematode with a six-celled thallus.

Fig. 27. Nuclear distribution in a sporangium.

Fig. 28. Emergence of zoospores.

Fig. 29. Germination in situ.

## PLATE 21



Myzocystium

accurate in their observations. Although Dangeard made a cytological study of the sporangia of *M. vermiculum*, he did not observe cleavage and maturation of the zoospores.

There is also some disagreement about the relative lengths of the flagella in this genus. Dangeard described the zoospores as heterocont in *M. vermiculum*, with the shorter cilium extending forward (fig. 20). None of the other investigators were very definite on this point, and it is impossible to determine with certainty from their drawings whether the zoospores are iso- or heterocont. In figure 47, for instance, Sparrow shows one flagellum to be slightly shorter, while in figure 48 they are more nearly equal in length.

The antheridia and oogonia may occur in the same thallus with the sporangia, but they usually do not appear in abundance until fairly late in the season. They are but modified segments of the thallus in the same sense as the sporangia and do not undergo any marked differentiation. The so-called antheridium is usually more elongate and cylindrical than the oogonium, but it is not so specialized a structure as in *Lagenidium*. According to Dangeard, the oogonium contains approximately eight nuclei, and no differentiation of an egg cell nor the formation of epiplasm occurs before fusion. In preparation for plasmogamy seven of the nuclei degenerate, leaving the oogonium uninucleate. Shortly before or at the time of fusion the protoplasm in the oogonium in *M. proliferum* contracts markedly (figs. 8, 9) around the tip of the conjugation canal according to Zopf. The antheridium, on the other hand, is binucleate (fig. 30), but only one nucleus functions in karyogamy. Prior to fusion a pore is formed in the wall between the two gametangia, or the antheridium sends forth a short tube into the oogonium (figs. 8, 9, 19, 37). The cytoplasm and one nucleus of the antheridium passes into the oogonium, and the two protoplasts fuse. The binucleate zygote begins to contract (fig. 31), and as the oospore wall begins to form karyogamy occurs (fig. 32). Dangeard's drawings and description are not very clear and convincing in relation to the critical stages of fusion, and further study of the behavior of the gametic nuclei is very essential. When an antheridium lies between two oogonia it is capable of fertilizing both, according to Dangeard.

After a period of rest the zygote nucleus divides and the oospore becomes multinucleate (fig. 34). Dangeard did not observe nuclear division, and nothing is known about when and where meiosis occurs. It presumably takes place during the first division of the oospore nucleus. Eventually the oospore develops an exit tube (fig. 35), but the formation of zoospores and their emergence have not been observed.

#### M. PROLIFERUM Schenk, l.c.

*Pythium proliferum* Schenk, 1859. (Not *P. proliferum* de Bary, 1860. Jahrb. Wiss. Bot. 2: 182.) Verh. Med. Gesell. Wurzburg 9: 27. Pl. 1, figs. 30-42, 47.

*P. globosum* Schenk, l.c., p. 27. Pl. 1, figs. 43-46.

- P. globosum* Walz, 1870 (pro parte) Bot. Zeit. 28: 556. Pl. 9, figs. 13-19.  
*Lagenidium globosum* Lindstedt, 1872. Synopsis d. Saproleg., p. 54.  
*M. globosum* (Schenk) Cornu, 1872. Ann. Sci. Nat. 5th ser. 15: 21.  
*Bericium transversum* Sorokin, 1883. Arch. Bot. Nord. France 2: 43. Fig. 46. 1889. Rev. Mycol. 11: 138. Pl. 78, fig. 76.  
*Bericium nase* Sorokin, 1883, p. 43, fig. 47; 1889, p. 138. Pl. 81, fig. 117.

Thallus usually elongate, unbranched and constricted; consisting of 1 to 20, usually less than 10, segments in a linear series. Sporangia hyaline, smooth, spherical, 8-25  $\mu$ , ellipsoidal, 13-16  $\mu \times$  16-26  $\mu$ , and elongate with a single, 2-6  $\mu \times$  4-48  $\mu$ , exit tube which may project for varying distances beyond the surface of the host cell. Zoospores bean-shaped, 3.6  $\times$  5.4  $\mu$ ; partially formed in the sporangium, emerging and developing further in an extramatrical vesicle, freed by the rupture or deliquescence of the latter. Gametangia occurring

#### PLATE 22

##### *M. vermiculum*

(All figures after Dangeard, '06)

Fig. 30. Two binucleate antheridia and two terminal multinucleate oogonia.

Fig. 31. Incipient oospore with gametic nuclei.

Fig. 32. Completion of karyogamy.

Fig. 33. Oospore in median section.

Fig. 34. Oospore with divided nuclei.

Fig. 35. Early germination stage.

##### *M. megastomum*

Fig. 36. Reduced thallus with elongate exit tubes. Wildeman, '96.

Fig. 37. Portion of thallus showing sporangia, oogonia, antheridia, and plasmogamy.

Fig. 38. *Ancylistes miurii* Skvortzow which possibly relates to *M. megastomum* Skvortzow. Skvortzow, '25.

Figs. 39, 40. Antheridia, oogonia (?) and oospores of *A. miurii* Skvortzow, l.c.

##### *M. zoophthorum* Sparrow, '36

Fig. 41. Infection stages.

Fig. 42. Young elongate thallus.

Fig. 43. Infected rotifer with numerous thalli, antheridia, oogonia, and oospores.

Figs. 44, 45. Stages in the emergence of the protoplasm from sporangium.

Fig. 46. Cleavage of initial globule of protoplasm into zoospores; additional fully formed zoospores emerging from neck of sporangium.

Figs. 47, 48. Dorsal and ventral view of zoospores.

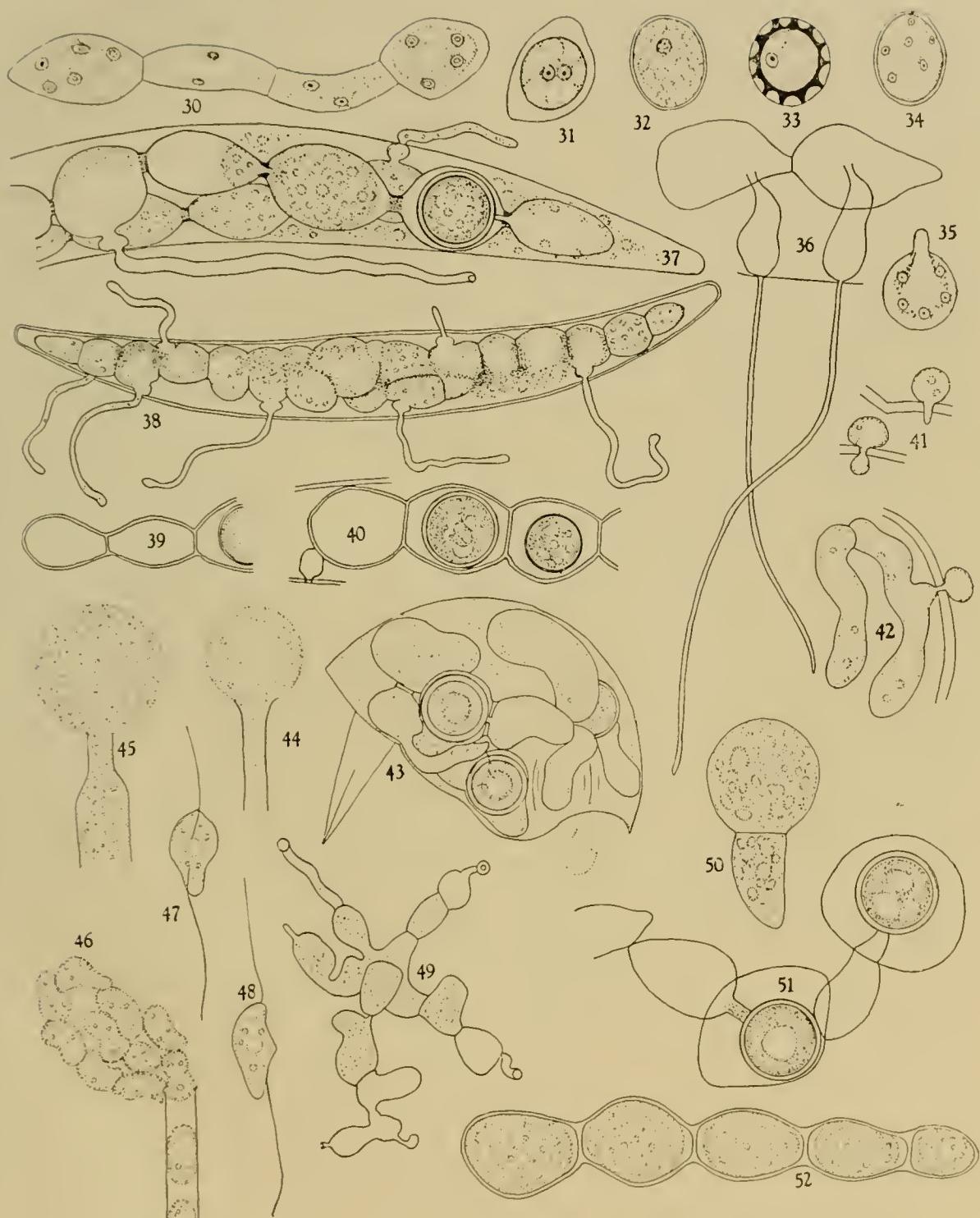
Fig. 49. Thallus of *M. irregularare* from *Microasterias* cell. Petersen, '10.

Fig. 50. Young antheridium and oogonium of *Myzocytium* (*Rhizomyxa hypogea* pro part) sp. (?) Borzi, '84.

Fig. 51. Oogonia with oospores, *Myzocytium* sp. (?) Borzi, l.c.

Fig. 52. *Myzocytium* sp. (?) from tobacco root cell. Preiszecker, '05.

## PLATE 22



Myzocytium

among the zoosporangia; oogonia spherical, 15–25  $\mu$ , oval, ellipsoidal and egg-shaped; antheridia fusiform, and elongate, 8–12  $\mu \times$  16  $\times$  18  $\mu$ , and narrowly spindle-shaped. Oospores spherical, 8–25  $\mu$ , ellipsoid, 14–22  $\mu$ , and somewhat angular, hyaline with a smooth thick, two-layered wall and a large eccentric refractive globule; germination unknown.

Parasitic in *Mougeotia* sp., *Mesocarpus* sp., and *M. pleurocarpus*, *Spirogyra* sp., *Zygnema* sp., *Cosmarium connatum*, *C. botrytis*, *Micrasterias rotata*, and *Closterium didymotocum* in Germany (Schenk, l.c.; Lindstedt, l.e.; Reinsch, '78; Zopf, '84; Schroepter, '86; Minden, '11); various algae in France (Cornu, '69); *Cladophora* sp. and *Arthrodesmus* sp. in Russia (Sorokin, '83, '89); *Spirogyra* sp., *Zygnema* sp., and *Cosmarium* sp. in Belgium (de Wildeman, '93, '95, '96); *Cladophora* sp. and *Spirogyra* sp. in Roumania (Constantineau, '01); *Mougeotia* sp. and a dead insect in Denmark (Petersen, '09, '10; Lind, '13); *Spirogyra* sp. in China (Skvortzow, '27), *Cladophora* sp., *C. kuetzingiana*, *Zygnema cruciatum*, *Mougeotia* sp., *Closterium acerosum* and *Spirogyra* sp. in Iowa, Montana, and New York, U. S. A. (Martin, '27; Graff, '28; Sparrow, '32, '33; Thompson, '34); *Spirogyra* sp. in Bulgaria (Valkanov, '31); *S. affinis* in India (Chaudhuri, '31; Mundkur, '38); *Spirogyra jurgensii*, *Spirogyra* sp., and *Cladophora* sp. in Japan (Tokunaga, '34); *Spirogyra* sp. and *Mougeotia* sp. in Hungary (Scherffel, '02; Domjan, '35); *Spirogyra* sp., *Mougeotia* sp., *Zygnema* sp., *Mesocarpus* sp., *Closterium leibleinii*, and *Closterium* sp. in Bohemia (Cejp, '32, '35).

This is the most widely distributed species of *Myzocytium*, but although it has been observed and described a great number of times, there are still numerous differences of opinion in the literature about certain of its developmental phases. Cornu, Walz, Zopf, Sparrow ('32) and Thompson claimed that the sporeplasm emerges through the exit tube and then undergoes cleavage into zoospores within a vesicle as in *Pythium*, while other investigators have maintained that the swarmspores are delimited to some degree in the sporangium, emerge singly in succession, and then complete their development in the extramatrical vesicle. Sparrow described the zoospores as only 3.6  $\times$  5.4  $\mu$  in size, but Constantineau claimed that they vary from 5  $\times$  6 to 6  $\times$  9  $\mu$ . This difference may be due to unequal and abnormal cleavage, whereby large zoospores are formed, as has been described by Thompson. The writer has often found abnormally large zoospores with four to twelve flagella.

Dwarf thalli consisting of one or two segments often occur in this species, and for this reason the author is inclined to agree with Fischer ('32), de Wildeman ('96), and Minden that Sorokin's *Bicerium transversum* and *B. naso* may possibly relate to this species. Petersen, however, was doubtful about the latter species' identity. It is to be noted here that the exit tubes of *B. naso* are inflated and globular at the base and extend far beyond the sur-

face of the host cell. If this character proves to be of specific diagnostic value *B. naso*, on the other hand, may possibly represent dwarf thalli of *M. megastomum*. Sorokin's *Olpidium tuba* and *O. saccatum* may also possibly be reduced specimens of *M. proliferum*. Cornu ('77) was of the opinion that the parasites which Reinsch (pl. 17, figs. 6–12) found in various desmids relate to this species also, but Zopf ('84) believed that the one with parthenogenetic oospores figured in *Closterium didymotocum* is not identical but only closely related to *M. proliferum*.

*Myzocytium irregulare* Petersen ('09, '10) which parasitizes *Micrasterias* and *Cosmarium* may possibly be nothing more than dwarf and irregular thalli of *M. proliferum*. This species is characterized primarily by irregular and lobed sporangia, the short exit tubes of which are greatly inflated inside of the host wall (fig. 49). Nothing is known about the structure and shape of the zoospores, gametangia and oospores. Petersen believed that all forms which had been previously described in flat and small desmids, exclusive of those in *Closterium*, relate to *M. irregulare*, and that of *M. proliferum* should include only the regular elongate and chain-like forms which occur in the filamentous algae and elongate desmids. He was further of the opinion that *M. irregulare* may also possibly relate to *Lagenidium* or represent a new genus. Chaudhuri supported the latter viewpoint, but Cejp ('33, '35), who found *M. irregulare* in *Micrasterias rotata*, *M. truncata*, *Cosmarium* sp., and *Pleurotaenium* sp. in Bohemia, thought it may relate to *Myzocytium*. So far sexual reproduction and oospores have not been observed. Until more is known about the life history of this parasite and extensive inoculation experiments have been made, the validity of Petersen's species remains doubtful.

*Myzocytium lineare* Cornu ('72, p. 21) is imperfectly known and very doubtful, and Minden was of the opinion that it relates to a species of *Lagenidium*. Cornu described it very briefly as simple and sparingly branched with elongate, linear sporangia, but he did not figure it. He ('77) also believed that the thalli shown in Reinsch's (l.e.) figures 5 and 14, plate 17, relate to *M. lineare*. The data relative to Cornu's fungus are too fragmentary to warrant any definite conclusions, so that the validity, identity, and synonymy of this form are largely a matter of personal interpretation.

#### M. VERMICOLUM (Zopf) Fischer, 1892. Rabenh. Kryptogfl. I. 4: 75.

*M. proliferum* var. *vermicolum* Zopf, 1884. Nova Acta Ksl. Leop.-Carol. Deut. Akad. Nat. 47: 167. Pl. 14, figs. 35–37.

*Bicerium lethale* Sorokin, 1883. Arch. Bot. Nord France 2: 37. Fig. 45. 1889. Rev. Mycol. 11: 138. Pl. 78, figs. 72–74.

Zoosporangia spherical, oval, ellipsoidal, irregular, lobed; occurring singly and isolated, in pairs, or up to 12 in a linear chain, with 1–2 wide exit tubes of variable length. Zoospores oval, heterocont (?).

short flagellum directed forward and the long one backward; delimited in an extramatrical vesicle (?) or formed within the sporangium and escaping singly in succession; germination *in situ* fairly common, forming a yeast-like bud in germination. Gametangia occurring among the zoosporangia; oogonia oval, egg-shaped and ellipsoidal; antheridia elongate, cylindrical and slightly spindle-shaped. Oospores spherical and ellipsoidal with a thin endospore and a stellate or polygonally-sculptured exospore; germinating by becoming transformed directly into a zoosporangium with an exit tube.

Parasitic in nematodes in Germany (Zopf, l.c.), Russia (Sorokin, l.c.), France (Dangeard, '06), and Bulgaria (Valkanow, '31).

According to Dangeard, this species is very abundant in France as a parasite of nematodes, occurs frequently in association with *Protascus subuliformis*, and may easily be mistaken for the latter species when the thalli are young and reduced in size. So far as the author is aware there are no measurements of the thallus, oogonia, antheridia and zoospores of this species to be found in the literature. Zopf listed *M. vermiculum* as a variety of *M. proliferum*, but Fischer raised the former to specific rank on the grounds that it parasitizes an entirely different group of organisms. No cross inoculations, however, have been made to determine whether or not *M. vermiculum* will parasitize algae.

Zopf reported that the zoospores are delimited in an extramatrical vesicle at the tip of the exit tube, while Dangeard described them as being fully formed within the sporangium. According to the latter worker a few of the swarmspores emerge in a small vesicle (fig. 28) which soon bursts and sets them free, while the remaining ones emerge singly and in succession. It is to be noted here that zoospore emission in *Myzocytium* sp., described by Thompson ('34) in *Spirogyra* sp., is very similar to that reported by Dangeard, with the exception that no small vesicle occurs around the initial emerging spores. Further study is accordingly necessary to determine which or if both of the reported methods of zoospore formation and emission occur. It is particularly noteworthy that Dangeard figured the zoospores as heterocont with the short cilium directed forward and the longer one backward (fig. 20), as in the case of secondary swarmers of *Lagenidium* species; whereas in other species of *Myzocytium* they are figured as isocont. In this respect also further study of this species is very essential.

Manpas' ('15) *M. polymorphum*, the thallus of which breaks up into free and independent sporangia at maturity, probably relates to this species. He merely mentioned it in relation to *Protascus* and apparently has never figured or described it further.

**M. MEGASTOMUM** Wildeman, 1893. Ann. Soc. Belge Micro. 17: 53. Pl. 6, figs. 6-10; pl. 7, figs. 19-20.

*Ancylistes miurii* Skvortzow, 1925. Arch. Protistk. 51: 432. Figs. 7-10.

Thallus at first cylindrical, 7.4-12  $\mu$  thick, unbranched; later becoming constricted and septate,

consisting of 5-18 ovoid, ellipsoid, elongate and somewhat cylindrical, 9-26  $\mu \times$  12-50  $\mu$ , segments with a single exit tube which is inflated, globular 3.7-4.2  $\mu$  in diameter, irregularly lageniform and appressorial-like inside of host wall, and may extend to a distance of 150  $\mu$  on the outside of host. Size, structure and behavior of zoospores unknown. Antheridia oval and spindle-shaped; oogonia oval, barrel-shaped, 12-19.5  $\mu \times$  7.4-12  $\mu$ ; oospores spherical, 7.4-13  $\mu$ , with a thick, hyaline, smooth wall and several refractive globules; germination unknown.

Parasitic in *Closterium attenuatum* and *Spirotaenia* sp. in Belgium (de Wildeman, '93, '95, '96); *Closterium* sp. in Manchuria (Skvortzow, l.c.); *Closterium* sp. and *Pleurotaneum trabecula* in Bohemia (Cejp, '35); *C. striolatum* and *C. areolatum* in North Carolina, U. S. A. (Berdan, '38).

Whether or not *M. megastomum* (de Wildeman) *forma* Skvortzow (l.c., p. 431), which occurs in *Closterium* sp. is a variety or form of de Wildeman's species is uncertain, but the writer is at present of the opinion that it is identical with the latter. It is characterized by globular and spherical, 12.9-22.5  $\mu$ , sporangia, 10-23.5  $\mu$  long exit tubes, and spherical, 11-13  $\mu$ , smooth, hyaline oospores.

*Ancylistes miurii* Skvortzow is possibly identical to de Wildeman's species also. The author is accordingly listing it as a synonym and presenting figures of its thallus and resting spores (figs. 38-40). As Miss Berdan has pointed out, the infection hyphae which Skvortzow figured may be nothing more than exit tubes for the emission of the zoospores. Until the presence of conidia and direct infection by hyphae have been demonstrated, Skvortzow's species will remain a doubtful species of either *Ancylistes* or *Myzocytium*.

**M. ZOOPHTHORUM** Sparrow, 1936. Jour. Linn. Soc. London, Bot. 50: 461. Pl. 19, figs. 1-14.

Thallus rarely branched, constricted or unconstricted, septations narrow and inconspicuous, segments 5-17  $\mu$  in diameter, variable in length. Zoosporangia irregular, sac-like and lobed with a single short exit tube. Zoospores 6-7  $\mu \times$  10-11  $\mu$ ; partially or wholly delimited within the sporangium, emerging in succession, and forming a subspherical mass at the mouth of the exit tube, which soon separates into irregular segments. Sexual fusion through a pore; oospores hyaline, smooth, thick-walled, spherical, 12-15  $\mu$ , with a large refractive globule; germination unknown.

Parasitic in rotifers and rotifer eggs in England and Denmark.

Sparrow was uncertain about the generic position of this species. In some respects it resembles reduced thalli of *M. vermiculum*, while in other instances the tubular, contorted segments are reminiscent of *L. pygmaeum*. In sexual reproduction, however, it is like *Myzocytium*. More recently ('39) Sparrow has pointed out its similarity to *L. oophilum* which also parasitizes rotifer eggs. The possi-

bility that it is not identical to the latter species thus remains to be shown.

Sparrow ('36, p. 463, fig. 4q) further described an elongate thallus consisting of a linear series of elliptical segments,  $20-22 \mu \times 18-20 \mu$ , connected by narrow cylindrical, refractive isthmuses in *Syne-dra* sp., which he believed may likewise relate to *Myzocytium*. He did not, however, observe any developmental and reproductive stages.

In connection with the above report of doubtful *Myzocytium* species it may be pointed out that Stein ('51, pl. 18, figs. 1-7; '59, pl. 4, figs. 49-55) figured an elongate body in *Vorticella microsoma* which he believed relates to the developmental cycle of this animal. At maturity this thallus becomes contorted and lobed and gives rise to bean-shaped spores in a spherical, extramatrical vesicle. The structure and appearance of the sporangia and spores suggest very strongly that they may relate to a species of *Myzocytium*. He ('59, pl. 1, fig. 9) also showed another vesicle with spores in *V. nebulifera* which may also possibly belong to a similar parasite.

Preissecker ('05, p. 3, fig. 43) figured and briefly described a linear series of oval pale golden cells in the roots of tobacco which he believed might represent a dwarf individual of *Myzocytium* sp., the largest cell of which measures  $28 \times 37 \mu$  (fig. 52). Zoospores and oospores were not observed. As Preissecker pointed out, the extremely thick walls of the cells militate against the possibility that this is a species of *Myzocytium*.

It is not improbable that the heterogamous sexual stages which Borzi ('84) included in the life cycle of *Rhizomyxa hypogaea* may relate to a root inhabiting species of *Myzocytium*. This is the viewpoint expressed by Schroeter ('97) and Minden ('11). More recently Barrett ('35) found similar sexual stages in association with a plasmodiophoraceous species in roots of *Stellaria media* and likewise concluded that they relate to a species of Lagenidiaceae. In view of these observations two of Borzi's figures have been included in plate 22 of *Myzocytium*.

Whether or not the fungus figured by Turner ('92) in *Oedogonium* sp. relates to *Myzocytium* or to the Lagenidiaceae is very doubtful. Superficially, it bears some resemblance to the thallus of *Myzocytium*, but the presence of several connecting isthmuses between adjacent segments militates against its inclusion in this genus.

## LAGENA

Vanterpool and Ledingham, 1930. Canad. Jour.

Res. 2: 177.

(PLATE 23)

Thalli intramatrical, unicellular, coenocytic, solitary or numerous, sac-shaped, oval, elongate, tubular, lobed and branched; attached to the host cell wall by a short neck the end of which fits into a thickened collar; transformed holocarpically into

zoosporangia or gametangia at maturity. Zoosporangia hyaline, smooth, and of the same shape as the thallus; content emerging at maturity through a short exit tube into an extramatrical vesicle and cleaving into zoospores. Zoospores bean-shaped, isocont, flagella inserted in a lateral depression. Male and female thalli fairly equal in size and usually indistinguishable, hyaline, smooth, oval or slightly elongate; conjugation canal of variable length, developed by the male thallus; no differentiation of an egg cell and periplasm; multiple fertilization rare. Oospores single or rarely numerous, hyaline, smooth, oval, spherical, thick-walled, simple or compound with one or two large refractive globules; germination unknown.

This monotypic genus has many characteristics in common with *Lagenidium*, *Myzocytium*, and *Pythium*. The isocont bean-shaped zoospores (fig. 8) have two laterally inserted flagella and the same characteristic method of swimming as in these genera, but sexual reproduction is predominantly iso-gamous. In germination the zoospores form an infection tube which penetrates the host cell wall (fig. 1), and after it has grown into the host cell its tip begins to enlarge and eventually develops into the mature thallus. The extramatrical zoospore case gradually disappears in the meantime, but the intramatrical portion of the germ tube remains attached to the thallus as a neck in contact with the host wall. A thick collar is formed around its upper end by the host cell wall at maturity, which gives it a characteristic appearance when viewed from above (figs. 2, 11-16).

The mature thalli may be comparatively small, oval and oblong as in *Olpidium* (figs. 1, 2) or greatly elongate, curved, lobed, branched, and hypha-like (fig. 3), as in *Lagenidium*. A single thallus may completely fill a host cell, or several small ones may be present in one cell. They may develop directly into

## PLATE 23

### *Lagena radicicola*

(Figs. 3, 17, and 18 drawn from photographs after Truscott; other figures after Vanterpool and Ledingham.)

Fig. 1. Stages of infection and development of the thallus.

Fig. 2. Two mature thalli and an empty sporangium.

Fig. 3. An elongate, tubular branched thallus.

Fig. 4. Mature sporangium with elongate exit tube.

Figs. 5-7. Stages of the emergence of the protoplasm into a vesicle and cleavage into zoospores.

Fig. 8. Rupture of vesicle and liberation of the zoospore.

Fig. 9. Encysted zoospore.

Fig. 10. Empty sporangium and an encysted zoospore on surface of host cell.

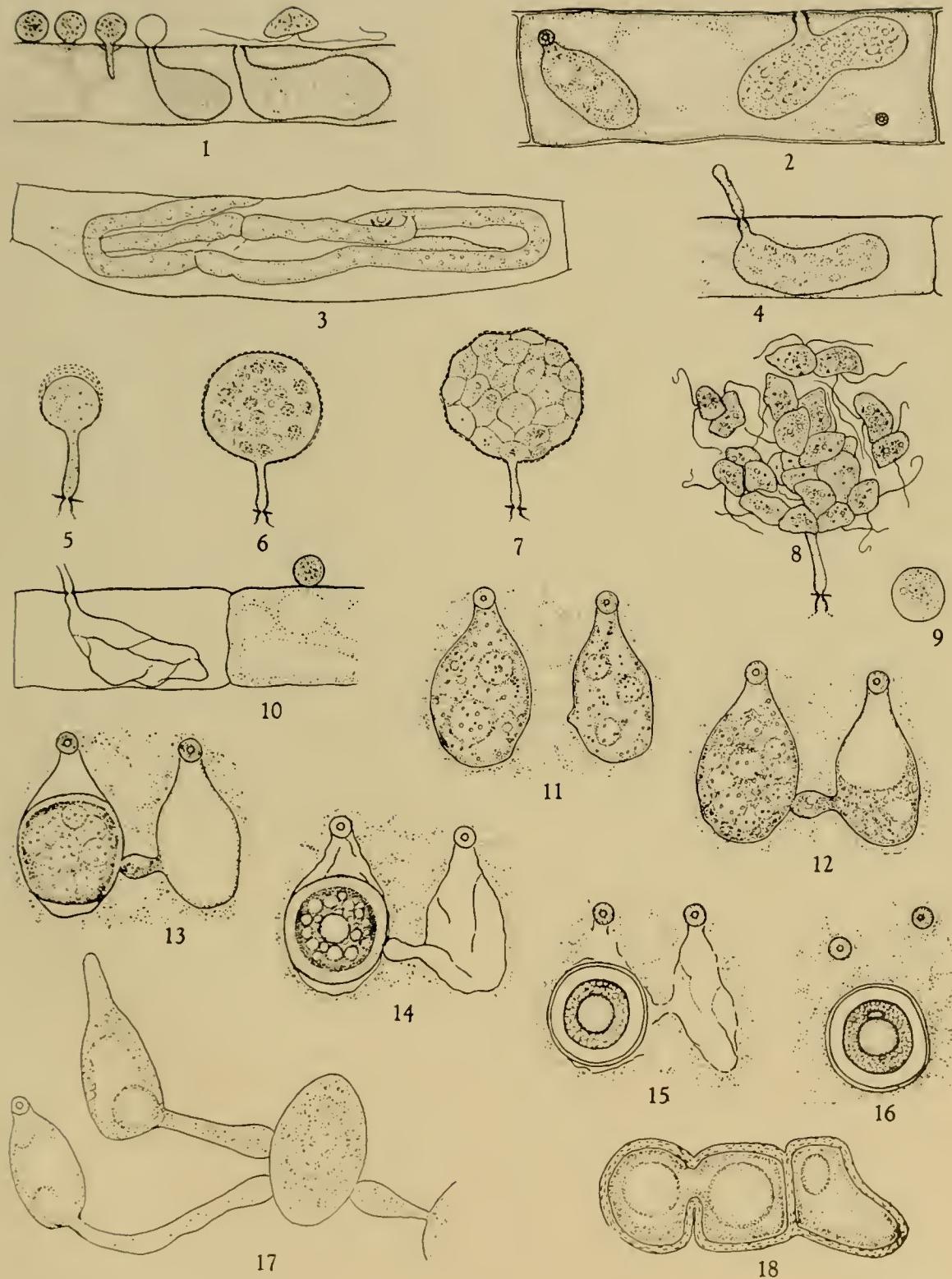
Figs. 11-15. Stages in oospore development; content of male thallus passing into female thallus.

Fig. 16. A free mature oospore.

Fig. 17. Multiple fusion; contents of three male thalli passing into one female thallus.

Fig. 18. Compound oospore.

## PLATE 23



zoosporangia or male and female gametangia. In the former case a short exit tube grows out from the neck of the thallus (fig. 4), and as the protoplasm begins to move out its tip gradually enlarges into a spherical vesicle into which the entire contents of the thallus emerges (figs. 5-6). Vanterpool and Ledingham regarded this vesicle as the sporangium proper and referred to the thallus which gives rise to it as a presporangium. The emerged mass of protoplasm soon begins to cleave progressively into segments (fig. 7), and the whole mass of zoospores shows the same movement and behavior as in *Pythium*.

Sexual fusion may occur between two or more thalli in the same cell. One of these, which is designated as the male, puts out a conjugation tube of variable length which fuses with a female thallus (figs. 12, 13, 17). If the two are almost in contact the tube may be reduced to a small swelling on the side of the male thallus at the point of contact with the female. The content of the male then passes very slowly into the female thallus (figs. 12, 13), where the combined protoplasts eventually contract and assume an oval or spherical shape (fig. 16). No delimitation or differentiation of an egg cell and periplasm occurs in the female thallus in preparation for fertilization, according to Vanterpool and Ledingham, but Truscott's ('33) report that several oospores may be formed in one female thallus suggests at least that division of the ooplasm may take place. On the other hand, division may possibly occur after fusion has been completed. A thick wall is eventually formed around the zygote, and after a short while the empty remains of the male and female thalli disintegrate, leaving the oospores free (fig. 16). Occasionally two or more male thalli may fuse with one female (fig. 17). The conjugants are multinucleate, according to Vanterpool and Ledingham, but nothing is known about the behavior of the gametic nuclei before and during fusion.

The formation of oospores may be increased by drying out the soil slightly, and Vanterpool and Ledingham therefore concluded that sex is largely determined by adverse environmental conditions. They described *Lagena* as dioecious but were uncertain whether the zoospores which give rise to male and female thalli respectively come from the same or different zoosporangia. They nonetheless assumed that zoospores from sporangia and germinated oospores may be of three types: i.e., + and —, —, and +, as shown in the diagram below.

Vanterpool and Ledingham emphasized the striking similarity of *Lagena* to reduced species of *Pythium* and *Lagenidium* and regarded it as a possible

connecting link between the Lagenidiaceae and Pythiaceae.

**L. RADICICOLA** Vanterpool and Ledingham, l.c. Pls. 1, 2, Figs. 3-7. Truscott, 1933. Mycologia 25: 263. Figs. 1-11.

Thalli  $14 \times 35 \mu$  or more, exit tubes  $4 \times 10-20 \mu$ ; zoospores  $7 \times 11 \mu$ ; oospores  $10-25 \mu$ . (For additional details see generic description above.)

Parasitic in roots of *Triticum aestivum*, *T. durum*, *Hordeum vulgare*, *Secale cereale*, *Agropyron repens*, *Zea mays*, and other wild grasses in Ontario and Saskatchewan, Canada.

According to Truscott, this species may occur on a number of wild grasses, but Vanterpool and Ledingham found it to be more limited in host range. *Avena sativa*, *A. factua*, *Agropyron Tenerum*, *A. spicatum*, *Bromus inermis*, *Poa compressa*, and *Sinapis arvensis* remained immune to attack when grown among infected wheat plants. *Lagena radicicola* causes a root disease which is characterized by stunted, curved roots. The fungus has a predilection for cells in the root tip, and its interference with nuclear and cell division doubtless leads to the shortening and curvature of the roots. Infected roots have yellowish-brown lesions in the region of infection and the root system as a whole is reduced. No enlargement of cells nor hypertrophy of roots have been observed. The stems of infected plants are considerably shorter than those of normal specimens, while the leaves become pale-green and lighter in color.

The thalli described by Truscott from Toronto were more elongate, cylindrical, tubular, and branched than those found by Vanterpool and Ledingham in Saskatchewan, and it is thus evident that the thallus of *L. radicicola* may vary markedly in size and shape. Truscott reported and figured compound oospores (fig. 18) and found evidence that as many as six oospores may possibly be formed in one female thallus.

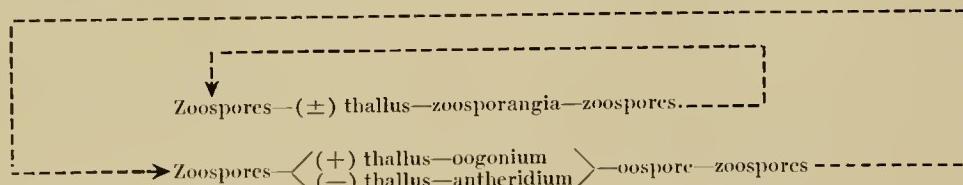
## DOUBTFUL GENERA

### RESTICULARIA

Dangeard, 1891. Le Bot. 2: 96.

(PLATE 24)

Thallus intra- and extramatrical, broadly elongate, tubular, vesicular and filamentous; irregular and undulating in contour, constricted at irregular intervals, with numerous short protuberances and



branches, confined to a single host filament or becoming extramatrical and infecting several algal threads. Zoosporangia not sharply differentiated (?), contents emerging as a mass and undergoing cleavage as in *Pythium* (?). Zoospores oval, laterally biflagellate and isocont. Sexual reproduction imperfectly known; two similar-sized protoplasts of adjacent swellings in the same thallus fusing to form spherical resting spores (oospores, zygospores?); germination unknown.

This genus was created by Dangeard for a filamentous parasite of *Lyngbya aestuarii* found in France. He placed *Resticularia* in the Lagenidiaceae (Ancylistales) close to *Lagenidium* and *Myzocytium*, but his description of its development and life cycle was meager and incomplete. As a result the identity and relationships of this genus have been the subject of much discussion and disagreement among systematists in mycology who are not particularly familiar with the Lagenidiaceae. Saccardo ('91, '12) followed Dangeard's disposition of this genus, but some mycologists (Minden, '11; Fitzpatrick, '30) regarded it as a doubtful member of this group, principally because of the observations of Fritsch ('03). Other mycologists (Fischer, '92; Wildeman, '96; Schroeter, '97; Fritsch, l.c.) have placed it next to *Ancylistes* and looked upon it as related to this genus or a transition form between the Lagenidiaceae and *Ancylistes*. The latter views of course antedate the discovery that *Ancylistes* belongs among the Entomophthorales and does not relate to the Lagenidiaceae.

Observations on a parasite found in *Lyngbya* in the laboratories at Columbia suggest that the organism found by Dangeard is a valid member of this family. This view is further supported by the recent discovery of Couch ('41) that the zoospores of *Resticularia* sp. are laterally biflagellate and isocont. However, the question of whether *Resticularia* should stand as a distinct genus or be merged with *Lagenidium* or *Myzocytium* remains to be answered. At present, the author is of the opinion that his fungus and probably Dangeard's *R. nodosa* relate to species of *Lagenidium*. Further studies on the method of sexual reproduction are necessary before this point can be settled. The author is further of the opinion that the fungus which Fritsch described as *R. nodosa* as well as *R. Boodlei* in species of *Tolyphothrix* do not relate to *Resticularia* in the sense of Dangeard. They are accordingly listed as doubtful or excluded species. Descriptions and illustrations of them are nevertheless included in plate 24 to make these data available to research students.

According to Dangeard, the zoospores are posteriorly uniflagellate, but it is not improbable that he may have overlooked a second flagellum of the type shown in figure 1. The large zoospores come to rest on the algal filament and form a broad germ or infection tube which penetrates the host cells (fig. 2). The tip of this tube elongates, increases in diameter, and eventually develops into the mature vegetative thallus (figs. 2-5) while the zoospore case remains

on the outside. At maturity the thallus may branch several times, grow out beyond the host, and infect other algal filaments. Whether or not it becomes septate is not obvious from Dangeard's description. The nuclei are rather evenly distributed along the length of the thallus (fig. 7, 8). No sharply differentiated zoosporangia were figured by Dangeard, which suggests that elongate segments of the thallus function in this capacity as in filamentous species of *Lagenidium*. At any rate the sporeplasm emerges through an exit tube (fig. 6) and undergoes cleavage into zoospores.

Very little is known about sexual reproduction, and no well-defined antheridia and oogonia have yet been described. According to Dangeard, the protoplasm in portions of the thallus contracts into two masses in adjacent swellings (fig. 9) which fuse to form oval, ellipsoidal, and spherical resting spores (figs. 10, 11). Inasmuch as the protoplasts as well as the swellings in which they accumulate are usually equal in size, Dangeard referred to the resting spores as zygospores. The type of spore formation shown in figure 9 is suggestive of sexual reproduction in *Myzocytium*, although intervening septa are lacking. Fischer was of the opinion that if Dangeard's account of sexual reproduction is correct *Resticularia* is to be regarded as a forerunner of the Zygomycetes.

#### R. NODOSA Dangeard, l.c. Pl. 4, figs. 25-31; pl. 5, figs. 3, 4.

Resting spores usually numerous, oval, ellipsoidal, elongate and spherical, 6-10  $\mu$  in diameter, contents coarsely granular with a large refractive globule, wall thick and double-layered. For additional details see generic diagnosis above.

Parasitic in *Lyngbya aestuarii* in France, killing the cells and causing the filaments to turn light yellow or colorless.

Fritsch found a similar looking fungus in *Tolyphothrix* in England which he took to be the same as Dangeard's species. The endophytic mycelium is comparatively coarse, 4-6  $\mu$ , irregular, frequently septate, and forms numerous brown, oval, spherical and ellipsoidal, 6-9  $\mu$ , thick-walled chlamydospores (figs. 12, 14), while the ectophytic mycelium is much finer, 0.5-1  $\mu$ , more branched, and bears single chlamydospores on short lateral branches (fig. 13). Fritsch believed that the zygospores described by Dangeard are nothing more than chlamydospores, the formation of which does not involve sexual fusion. While the endophytic mycelium of Fritsch's fungus resembles the thallus of *R. nodosa*, it possibly does not relate to Dangeard's species at all since Fritsch failed to observe zoosporangia or zoospores. Whether the fungus reported by Sparrow ('32) in filaments of *Tolyphothrix* in Massachusetts relates to *R. nodosa* or Fritsch's organism is uncertain because neither zoosporangia and zoospores nor sexual reproduction were observed.

*Resticularia Boodlei* is apparently further removed from Dangeard's species than the two above-

mentioned fungi. The endophytic mycelium is nevertheless irregular, 5–8  $\mu$ , with occasional septa (figs. 16–20) as in the previous species, but the ectophytic mycelium, 1.5–5  $\mu$  in diameter, is highly branched, septate, and bears numerous thin-walled conidia (12–15  $\mu$  in diameter) in chains on lateral branches (fig. 15). Zoosporangia, zoospores, resting spores, and chlamydospores are unknown.

Whether or not *R. Oedogonii* Skvortzow ('25, p. 432, fig. 14) is a valid lagenidiaceous species is uncertain at present. This species parasitizes *Oedogonium* sp. in North Manchuria and is characterized by a branched, hyaline, fine, 1–17  $\mu$  thick endophytic and a sparse ectophytic mycelium. The resting spores are hyaline, smooth-walled, 11.5–18.5  $\mu$  long by 7.4–11.1  $\mu$  wide, and contain a large refractive globule. Zoosporangia and zoospores have not been observed.

## EXCLUDED GENERA

### ACHLYOGETON

Schenk, 1859. Bot. Zeit. 17: 399.

Thallus intramatrical, usually elongate and septate, consisting of a chain or linear series of fairly short oval, ellipsoidal, egg- and spindle-shaped segments with truncate ends; constricted at the septa; rarely dwarfed and unicellular, holocarpic. Sporangia of the same size and shape as the thallus segments or unicellular thalli, with one exit tube of variable length which may or may not be inflated before passing through the host wall, extending a short distance beyond surface of host. Zoospores delimited in the sporangium; diplanetic, emerging singly in succession, and encysting in a loose cluster at the mouth of the exit tube as in *Achlyya*; emerging from the individual cysts and swimming away; posteriorly uniflagellate (?) with a small refractive globule. Resting spores (doubtful) formed asexually (?) by the contraction and encystment of the cell content; germination unknown.

The development and structure of the vegetative thallus are so strikingly similar to *Myzocytium* that it is very difficult to avoid a suspicion that Schenk may have been incorrect about the number, relative lengths and insertion of the flagella on the zoospores. This possibility is further suggested by the fact that he figured the swarmspores of *Myzocytium*, *Lagenidium*, and *Pythium* as uniflagellate also. Although Martin and Tokunaga saw encysted zoospores, they unfortunately did not determine the number of flagella and thus settle this important question. It is to be noted in this connection that the zoospores of *Lagenidium Oedogonii* also may encyst in a cluster at the mouth of the exit tube, which shows that such a character is common to the Lagenidiaceae and is in itself no basis for excluding *Achlyogeton* from this family. Should the zoospores prove to be bean-

shaped and laterally biflagellate *Achlyogeton* might well be merged with *Myzocytium* provided both genera are also similar in type of sexual reproduction. The presence of posteriorly uniflagellate zoospores with a single refractive globule and the lack of antheridia and oogonia at present militate against this view. *Achlyogeton* is accordingly excluded from the Lagenidiaceae for the time being. It may be noted here that its thallus resembles that of *Septolpidium* which is likewise characterized by uniflagellate zoospores. The latter, however, do not encyst at the mouth of the exit tube as in *Achlyogeton* but swim away after a brief pause—a characteristic which precludes close relationship with the latter genus, according to Sparrow ('36). Six years later, however, Sparrow ('42) reversed his opinion about this characteristic and included *Achlyogeton* with *Septolpidium* and *Biciricum* in a new family, the Achlyogetonaceae, of the Chytridiales.

### A. ENTOPHYTUM Schenk, i.e. Pl. 13, figs. A1–8.

Thallus composed of one to 15 segments. Sporangia oval, broadly ellipsoidal and egg-shaped with truncate ends, 15.6–33.6  $\mu$   $\times$  9.6–20.4  $\mu$ ; exit tubes 27–60  $\mu$   $\times$  3.6  $\mu$ . Primary zoospores elongate as they emerge; cysts spherical, 4  $\mu$ ; secondary swarmer more oval, rounded at the anterior and tapering slightly at the posterior end; flagellum approximately three times the length of the spore. Resting spores hyaline, smooth, oval and spherical.

Parasitic in *Cladophora* sp. in Germany (Schenk, i.e.); *Cladophora* sp. and *Anguillula* sp. in Russia

#### PLATE 24

(Fig. 1 after Couch, '41; figs. 2–11 after Dangeard, '91; figs. 12–20 after Fritsch, '03.)

Fig. 1. Laterally biflagellate isocont zoospore of *Resticularia* sp.; anterior flagellum with tinsel; posterior flagellum with tail piece.

#### *R. nodosa*

Fig. 2. Germination of zoospore and infection of *Lyngbya* filament.

Figs. 3, 4. Later developmental stages of thallus.

Fig. 5. Coarse irregular branched thallus.

Fig. 6. Emerged vesicular mass of protoplasm prior to cleavage; encysted zoospore above.

Fig. 7, 8. Distribution of nuclei in thallus.

Fig. 9. Plasmogamy of adjacent protoplasts in oospore (zygospore) development.

Figs. 10, 11. Young and mature oospores (zygospores).

Fig. 12. Mycelium with internal chlamydospore.

Fig. 13. Stages in chlamydospore formation.

Fig. 14. Mature chlamydospores.

#### *R. boodei*

Fig. 15. Extramatrical mycelium with spores.

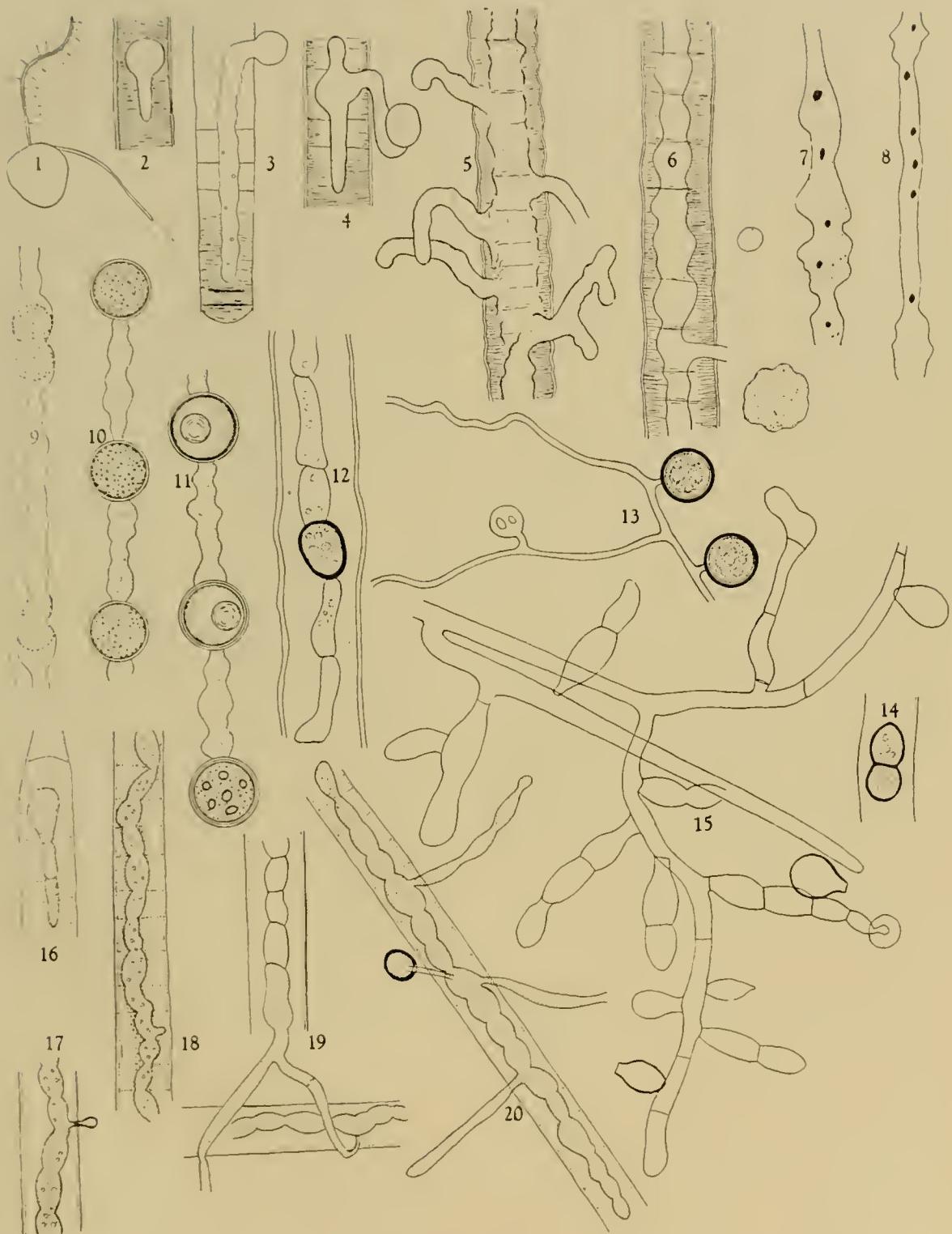
Fig. 16. Young thallus from germinated spore.

Figs. 17, 18. Intramatrical mycelium.

Fig. 19. Infection of two *Tolyphothrix* filaments.

Fig. 20. Thallus with germinated spore and three infection hyphae.

## PLATE 24



Resticularia

(Sorokin, '76, '83, '89); *Cladophora* sp. in Iowa, U. S. A. (Martin, '27) and Japan (Tokunaga, '31).

The thalli which Sorokin ('76) figured in *Anguillula* are somewhat similar to those of *Myzocytium*, and there is accordingly the possibility that he may have confused this species with *M. vermiculatum*. He is the only one to have reported *A. entophysum* on hosts outside of *Cladophora*. He nevertheless reported that the zoospores encyst in a cluster at the mouth of the exit tube in the same manner reported by Schenk, although he did not illustrate them.

Tokunaga found resting spores accompanied by a small, spherical, hyaline companion cell which he believed may relate to a species of *Olpidiopsis* parasitic in *Achlyogeton*.

*Achlyogeton solatium* Cornu ('70), parasitic in *Oedogonium obsidionale*, is imperfectly known, very doubtful, and has never been figured. Its thallus is filamentous, branched, and apparently extends through several host cells. The sporangia are delimited at irregular intervals along the thallus and form a single exit tube which is seven to eight times the diameter of the host cell in length. Three to twelve zoospores emerge from the sporangia and encyst in a cluster at the mouth of the exit tube, and after a while they emerge leaving the cysts behind as in *Achlyya*. In addition, Cornu, reported the presence of an extremely irregular, cylindrical oogonium with one to several oospores, but he did not observe the character of the antheridium. Fischer ('92) regarded Cornu's fungus as a species of *Pythium*, while Minden disregarded it entirely.

*Achlyogeton rostratum* Sorokin ('76) is a doubtful species. It parasitizes *Anguillula* and consists of chains of short oval segments or sporangia,  $5-6 \mu \times 7-9 \mu$ , with one straight, curved, or tortuous exit tube which becomes markedly inflated before passing through the host wall (figs. 11, 12). Zoospores and resting spores are unknown. Inasmuch as Sorokin did not observe the zoospores and their behavior, the relation of this species to *Achlyogeton* is questionable. The thalli shown in his figures are fundamentally similar to those of *Myzocytium* and may equally well relate to that genus. The inflation of the exit tube is not a distinctive specific character since Schenk has shown that it may occur in *A. entophysum* also.

*Achlyogeton salinum* Dangeard ('32) which parasitizes the marine algae *Cladophora laetevirens* and *C. flavaescens* in France is likewise too little known to ascertain its identity and validity as a member of this genus. Dangeard observed only developing and mature thalli, including sporangia and quiescent zoospores; so that nothing is known about the number, relative lengths, and position of the flagella in this species as well as its method of sexual reproduction. The mature thalli (figs. 13, 14) are strikingly similar to those of *A. entophysum* which parasitizes a fresh-water species of *Cladophora*. On the other hand, they are also similar to the thalli of *Myzocytium* and may equally well relate to a species of this genus.

## PROTASCUS

Dangeard, 1903. C. R. Acad. Sci. Paris 136: 628. (Not *Protascus* Wolk, 1913.)

(PLATE 25)

Thalli intramatrical, single or numerous, elongate, cylindrical, unbranched and unconstricted, straight or curved, and septate; segments separating at maturity and with further growth becoming transformed into sporangia and gametangia. Sporangia cylindrical, flask-shaped, uteriform, pyriform, and slightly irregular, usually with a single curved or straight short tapering exit tube which may end almost flush with the surface of the host cell or extend for a short distance beyond. Spores, non-motile, slightly curved and clavate, forcibly ejected from the sporangia; adhering to the host cell for some time after germination. Gametangia occurring among sporangia, unicellular, holocarpic, unequal in size, formed from the same or different thalli; conjugation usually lateral, sometimes scalariform or end to end; both gametangia contributing to the formation of the conjugation canal; contents of the larger female and smaller male gametangia often contracting toward the canal before plasmogamy; no differentiation of an egg cell and periplasm; protoplast of male flowing into the female gametangium and fusing with the ooplasm. Resting spores rarely parthenogenetic, lying free in the female gametangium, spherical and smooth with a fatty granular content which gives it a blackish, opaque appearance; germination unknown.

In ignorance of its method of sexual reproduction Dangeard placed this genus among the Hemiascales because of its non-motile spores and the manner in which they are ejected from the sporangium. At the same time he called attention to the similarity of its thallus to those of *Myzocytium* and *Lagenidium*. In his opinion *Protascus* may possibly be a transitional genus between the Phycomycetes and higher Ascomycetes. Since the discovery of its phycomycetous type of sexual reproduction by Maupas, however, Dangeard's views are no longer tenable. Maupas called the resting spores, zygospores, but pointed out the similarity of their method of formation to that of the oospores of *Myzocytium*. He regarded *Protascus* as a possible member of Fischer's Merolpidiaceae, the direction of growth of which has become distinctly oriented by its elongate host. Maire, on the other hand, assigned it to a position between the Lagenidiaceae and what was formerly known as the Aneylistaceae and proposed a new family, Protascaceae, to include it. Fitzpatrick regarded the resting spore as an oospore but was doubtful about the relationship of *Protascus* with the Lagenidiaceae. The lack of zoospores sharply delimits this genus from the Lagenidiaceae as the family is now recognized, and it is accordingly excluded. However, inasmuch as it has often been described in relation to *Lagenidium*, *Myzocytium*, etc., the author

feels that the following brief description is warranted.

According to Dangeard and Maupas, this parasite may occur in great abundance and can be easily cultured in living nematodes for a long time. The spores are predaceous, retain their vitality for a long time, and up to 15 days they are capable of infecting nematodes with which they come in contact. The slender end of the spore apparently is adhesive, since it is at this end that it becomes stuck to the nematode as the latter brushes against it. In spite of the squirming and writhing of the host, the spores remain attached in this position and soon germinate. They send a fine,  $0.3\text{--}0.4\ \mu$ , germ tube through the cuticle into the nematode (figs. 5, 6), and as the content of the spore passes into its tip it swells into a globular structure. This elongates in a linear direction and becomes filamentous. The young thallus is first uninucleate (fig. 9) but very shortly the primary nucleus undergoes division. These divisions are simultaneous, so that a large number of mitotic figures in the same stage may be found in the large sporangia (figs. 12, 13). Dangeard was not certain whether division is direct or indirect, but his figures indicate that it is mitotic.

After the thallus has attained its mature length, it divides by transverse walls into two to ten fairly equal segments (fig. 11). These soon separate at the septa, become free, and with further increase in length and diameter are transformed into either sporangia or gametangia. Dangeard's description and figures suggest that dwarf unicellular thalli may also be formed as in *Lagenidium* and *Myzocytium*. The details of cytokinesis and sporogenesis are not well known in spite of Dangeard's description. The incipient sporangia usually possess several small vacuoles which apparently coalesce to form a large central one as they mature (fig. 13), and the nuclei lie in the primordial utricle surrounding the vacuole. The spores are doubtless delimited by progressive cleavage as in other sporangia, and with maturity become clavate and oriented with the thick rounded end directed toward the exit tube (fig. 14). The latter may be straight, curved, or bent at right angles to the surface of the sporangium. As the neck of the sporangium perforates the host wall and deliquesces, the spores are all forcibly ejected at one time or in successive groups from the sporangium (fig. 15).

In some respects sexual reproduction is similar to that of *Myzocytium* and *Lagena*. Since conjugation is predominantly lateral (fig. 16) Maupas believed that most of the male and female gametangia are segments of different thalli. Heterothallism has not, however, been definitely established. End to end or scalariform conjugation may also occur (fig. 18), which suggests that the respective gametangia have arisen from the same thallus. The segments which are to become gametangia do not usually increase much in size, and are frequently elongate and cylindrical. Since the resting spore develops in the larger of the two gametangia and the content of the smaller is mobile, the two have been designated as male and

female respectively. Each sends out a protuberance toward the other as in some species of *Spirogyna* and as these come in contact they fuse at the tips. The content of each gametangium then usually contracts toward this common canal, and as the intervening wall breaks down the male gamete slowly passes over into the female gametangium and fuses with the ooplasm. No differentiation of an egg cell and periplasm has so far been observed, but the contraction of germ plasms toward the conjugation tube seems somewhat similar to that described by Zopf in *Lagenidium rabenhorstii*. Furthermore, conjugation in *Protascus* is also similar to sexual reproduction in *Lagena*, with the exception that in the latter genus the gametangia are usually equal in size and indistinguishable, and the conjugation tube is formed exclusively by the male.

The zygote soon becomes invested with a thick wall and goes into the resting condition (figs. 17-20). As noted above, Maupas called it a zygosporae, while Fitzpatrick referred to it as an oospore. Since reproduction is to a slight degree heterogamous, and the resting spore lies free in the female gametangium, the latter's terminology is perhaps more descriptive. The writer is nonetheless using the non-committal term, resting spore, for the time being, since the relationships of *Protaseus* are still obscure. No cytological study of sexual reproduction from fixed and stained material has yet been made, and it is not known whether the gametes are uni- or multinucleate at the time of fusion.

The presence of the parasite does not hinder the activities of its host and produce any marked pathological effects until after two or three days. By this time, however, the nematode gradually loses its ability to contract and move and becomes slow and heavy. Later as paralysis becomes more marked it undergoes tetanic contractions which last for a long time. In the end a final violent contraction occurs which leaves the animal in a stiff, rigid, twisted position. In a short while it begins to distend and straighten out as death occurs.

#### P. SUBULIFORMIS Dangeard, I.e. 1906. I.e Bot. 9: 256. Pls. 15-16.

*P. subuliformis* var. *maupasii* Maire, 1915. Bull. Soc. Hist. Nat. Afrique Nord. 6: 50.

Thallus  $5\text{--}10\ \mu \times 100\text{--}400\ \mu$ ; sporangia  $6\text{--}7\ \mu \times 16\text{--}110\ \mu$ , irregular ones up to  $26\text{--}28\ \mu$  in diameter; spores  $8\text{--}200$  in a sporangium,  $0.6\text{--}3\ \mu \times 20\text{--}25\ \mu$ , apparently adhesive at the slender end; gametangia usually slightly smaller than the sporangia; resting spores  $15\text{--}30\ \mu$  in diameter, wall  $1\text{--}2\ \mu$  thick. (For further details see the generic analysis above.)

Parasitic in nematodes in France (Dangeard, I.e.); *Rhabditis teres*, *R. giardi*, and *R. dolichura* in Algiers (Maupas, '15).

Maupas' attempts to infect *Cosmarium* sp., *Closterium lunula*, *Cladophora* sp., and *Stigeoclonium* sp. as well as numerous nematodes including *Diplogaster striatus*, *D. gracilis*, *Cephaloleus rigidus* and

*Rhabditis monohystera* with this parasite were unsuccessful, and his results suggest that *P. subuliformis* may have a limited host range.

It seems doubtful that Dangeard's species is different from Maupas' fungus, as Maire has suggested. The predominantly unicellular thalli which he describes and figures relate perhaps to segments of a longer thallus which have separated.

## MITOCHYTRIDIUM

Dangeard, 1911. Bull. Soc. Mycol. France 27: 202.

This genus was created for a single intramaterial species, *M. ramosum*, which parasitizes desmids of the genus *Docidium*. Dangeard regarded this species as intermediate between the Chytridiaceae and Acanthostaceae, but Butler ('28) was of the opinion that it should be included in the Cladochytriaceae, close to *Catenaria*. Couch's ('35) discovery of this species in North Carolina and his confirmation of the presence of rhizoids and posteriorly uniflagellate zoospores justifies Butler's view, in the author's opinion.

## RHIZOMYXA

Borzi, 1884. Rhizomyxa, nuovo ficomicete, Messina.

This genus has been fully discussed by the present author in his book on the Plasmodiophorales, 1942, and need not be treated further at this point. See discussion under *Myzocytium* also.

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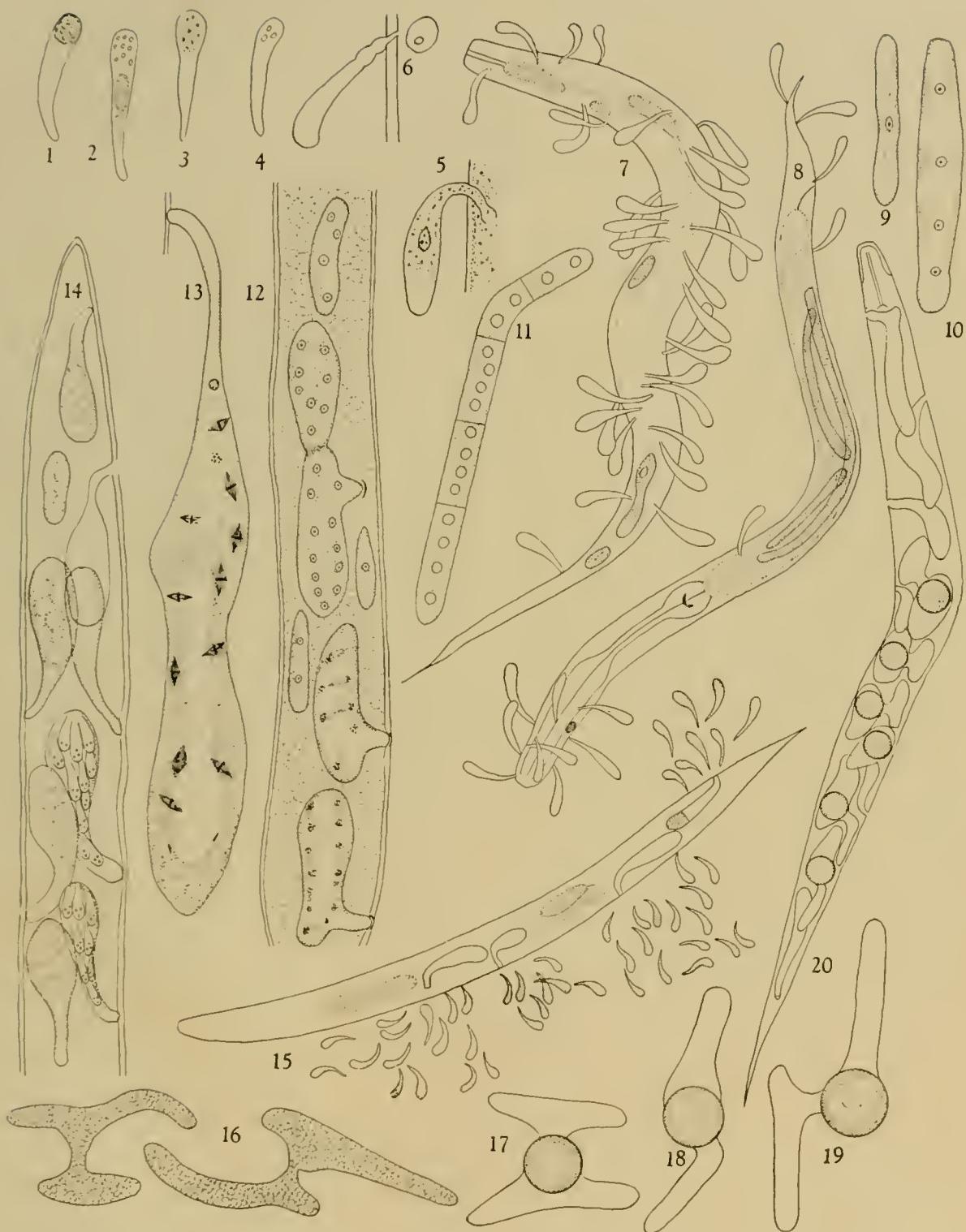
### PLATE 25

#### *Protascus subuliformis*

(Figs. 4, 5, 9, 10, 12–14 after Dangeard, '06; figs. 1–3, 7, 8, 11, 15–20 after Maupas, '15.)

- Figs. 1–4. Spores with refractive adhesive (?) content.
- Fig. 5. Early infection stage; content of uninucleate spore passing into host.
- Fig. 6. Later stage; parasite lying in host as an oval globule.
- Fig. 7. Heavily infected nematode with numerous attached spore cases and several thalli within.
- Fig. 8. Nematode with three elongate thalli.
- Figs. 9, 10. Uni- and tetranucleate thalli.
- Fig. 11. Elongate, curved, segmented, vacuolate thallus.
- Fig. 12. Separation of multinucleate thallus segments and their transformation into sporangia.
- Fig. 13. Mitosis in a sporangium.
- Fig. 14. Nematode with numerous sporangia, two of which are about to expel the spores.
- Fig. 15. Expelled comma-like spores.
- Fig. 16. Early stages in fusion of thallus segments connected by fusion canals.
- Figs. 17–19. Zygospores.
- Fig. 20. Nematode with numerous empty sporangia and zygospores.

## PLATE 25



Protascus

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## Chapter VII

### Phylogeny

DISCUSSIONS of phylogeny at any given period of time must obviously be based on existing knowledge and data relative to the group of organisms in question. Relationships which thus seem obvious at present may be completely invalidated by future studies and discoveries. Therefore, very few definite conclusions can be drawn at present about the origin and evolution of these holobiflagellate Phycomycetes as a whole because so little is known about the critical developmental stages of many of the genera and species. The present discussion will accordingly be confined to pointing out similarities and differences between these fungi, the lower organisms and higher fungi with which they appear to be related. Since it is not certain that all of the families described in the previous chapters constitute a natural phylogenetic series of closely related species, differences in origin and relationship are to be expected. As has been briefly noted before, these relationships involve principally the Proteomyxa or Monadineae, Plasmodiophorales, Saprolegniales, and Peronosporales and are based on similarities or differences in thallus structure, type of development, relative lengths and position of flagella, diplokontism, presence of cellulose in the cell walls, and type of sexual reproduction. Present day evidence suggests very strongly that most of these holobiflagellomycetes are either remotely or closely related to the higher Phycomycetes. However, it is not clearly evident whether they are primitive or reduced and degenerate, and many of the controversies on phylogeny in the past have centered on these questions. While the views of the early mycologists in this respect do not relate to groups as specific as those included in these so-called holobiflagellomycetes, they nonetheless apply here in a general sense. DeBary ('81, '84), Tavel ('92), Gäumann ('26), Gäumann and Dodge ('28), Mez ('29), Wettstein ('35) among others regarded most of the biflagellate species as reduced and degenerate oomycetous fungi resulting from their assumption of a parasitic mode of life. On the other hand, Dangeard ('86, '06), Lotsy ('07), Vuillemin ('08), Atkinson ('09), Cavers ('15), Scherffel ('25), Fitzpatrick ('30), Cook ('28), Bessey ('42), and others believed that

they are primitive and represent an ascending evolutionary line. Lotsy and Bessey suggested that they may have been derived from the Isoeontae and unicellular Heterokontae, respectively. Atkinson did not attach much significance to the number of flagella and derived them from the Chytridiales. Dangeard, Cavers, Scherffel, and Cook, however, believed that together with the Chytridiales they originated from the zoosporic Monadineae or Proteomyxa.

The evidence bearing on the origin and relationships of these holobiflagellomycetes will now be considered in greater detail. The provisional family, Woroninaeae, interpreted as a convenient dumping ground or a heterogeneous collection of genera which are quite probably unrelated, appears to be the most primitive and stands somewhat apart from the other families because its vegetative thallus is reported to be plasmodial in structure and mode of nutrition. As noted before, in *Woronina* the plasmodium cleaves into segments which are transformed directly into zoosporangia or resting spores. These structures may be united into compact sporangio- and cystosori, respectively, in *W. polycystis*, while in *W. glomerata* they lie comparatively loose and free. The striking similarity in type of development of these species to that of the Plasmodiophorales is obvious. Zopf ('94), Maire and Tison ('11), and Winge ('13) and others early recognized this similarity and stressed the relationship of *W. polycystis* to *Ligniera* and other genera of the Plasmodiophoraceae. This relationship was further emphasized by Ledingham's ('33, '39) and Couéh's ('39) discoveries of *Polymyxa* and *Octomyxa*, respectively. The latter genus, particularly, is almost identical in life cycle to *W. polycystis*, as was stressed by the present writer ('42) in his book on the Plasmodiophorales. Sparrow ('42) included *Woronina* in the latter order and discarded the family name Woroninaeae altogether. As has been stated already, future studies may possibly prove that *W. polycystis* is a species of the Plasmodiophorales, but so far as is now known, it differs in several respects from the valid members of this order. In the first place, it is not definitely known whether the zoospores are iso- or heterokont and whether the flagella are lateral or

anterior in position. Secondly, schizogony of the plasmodium has not been reported in *W. polycystis*, and nothing is known about the types of nuclear divisions in the vegetative and sporogenous thalli. Schizogony and the occurrence of "promitosis" are claimed to be outstanding characteristics of the Plasmodiophorales. Thirdly, the sporangia and resting spores of *W. polycystis* give a positive cellulose reaction when tested with chloro-iodide of zinc, while those of the Plasmodiophorales do not. Furthermore, in germination the content of the zoospore enters the host directly through a penetration tube, leaving the empty spore case on the outside of the host cell as in *Olpidiopsis*, *Rozellopsis* and other similar genera. In the Plasmodiophorales, on the other hand, the zoospores are reported to enter the host directly as a naked amoeboid body. How significant these minor differences are in phylogeny and whether or not they outweigh the similarities in thallus structure and type of development remains to be seen from future studies. Nevertheless, the presence or absence of cellulose is regarded as fundamentally significant by many students of phylogeny and evolution. *Woronina glomerata* differs from the previous species in several ways. Instead of forming but one zoospore in germination as in *W. polycystis* and the plasmodiophoraceous species, the resting spore functions as a sporangium and produces a large number of zoospores. Furthermore, the plasmodium is animal-like in mode of nutrition, according to Zopf ('94) and Scherffel ('25), and engulfs plastids, starch grains, and other solid bodies. This material is digested in well-defined food vacuoles, and the extraneous waste material is discarded to the outside in preparation for sporogenesis. This type of feeding and digestion is characteristic of the Proteomyxa, and for this reason Zopf and Scherffel relegated *W. glomerata* to the zoosporic group of the Myxozoidia or Proteomyxa. Thus, within the same genus, as *Woronina* is now interpreted, occur species with seemingly diverse relationships. However, these differences of relationship may not prove to be as significant as they now appear, because evidence is accumulating which suggests that certain species of the Proteomyxa, Plasmodiophorales, and *Woronina* may possibly be closely related.

Turning to the other two genera, *Pyrrhosorus* and *Rozellopsis*, which are temporarily included in the Woroninaceae, it becomes evident that the relationships are not well defined. Zoosporangia and resting spores apparently do not occur in *Pyrrhosorus*. Instead, the plasmodium cleaves into spore mother cells which unite into a sorus and later undergo three divisions, forming eight free spores. The latter are transformed directly into biflagellate isocont zoospores. Despite these differences the presence of a plasmodium and sorus suggests some degree of relation to or parallelism in development with the Plasmodiophorales. Juel ('01) was uncertain of the relationship of *Pyrrhosorus*, but he emphasized the striking similarity of its method of

spore development to that of *Tetramyxa*. As the writer ('42) has already pointed out, had *Octomyxa* been known at that time, Juel would doubtless have emphasized the relationship of his fungus with the Plasmodiophorales even more strongly. Winge ('13) also regarded it as closely related to the Plasmodiophoraceae and made extensive comparisons between its life cycle and that of *Sorolpidium*. He considered the sporangiosori of the latter genus as homologous with the sori of spore mother cells of *Pyrrhosorus* and believed that the absence of walls around the spore mother cells is of minor significance. Cook ('33), on the other hand, believed that the relation of this genus to the Plasmodiophorales is very questionable.

The origin and relationships of the provisional genus *Rozellopsis* are even more obscure. Compact or loose sporangio- and cystosori are unknown, and the only significant characters which it has in common with the two previous genera are its plasmodium-like vegetative thallus, which may or may not undergo schizogony or division, and biflagellate zoospores. Since the presence of a plasmodium has not been conclusively demonstrated in this genus, the inclusion of *Rozellopsis* in the same family with *Woronina* and *Pyrrhosorus* becomes even more questionable. However, the anteriorly biflagellate heterocont zoospores of *R. simulans*, according to Tokunaga's ('33) drawings, are strikingly similar to those of the Plasmodiophorales, but in infecting the host they behave like those of *W. polycystis*, *Olpidiopsis*, *Ectrogella*, etc. Instead of entering the host directly, they form an infection tube through which their content passes into the host cells. On the other hand, the structure and development of the thallus and resting spores in the aseptigenous and septigenous species are identical to those of the mono- and poly-sporangiate species, respectively, of the chytrid genus, *Rozella* and *Pringsheimella dioica*, as far as is now known. Whether this indicates merely a parallelism in development from different ancestors or direct relationship is not certain. According to Bessey's ('42) theory of origin through the retention or loss of the second flagellum, *Rozellopsis* is more primitive than *Rozella* and *Pringsheimella* and may have given rise to these genera by the loss of one flagellum. While this theory seems plausible, it is obvious that the loss of one flagellum, without change in position of the remaining one, from the zoospore of *Rozellopsis* would not lead directly to the distinctly posteriorly uniflagellate zoospore of *Rozella* and *Pringsheimella*, since both flagella in *Rozellopsis* are reported to be either lateral or anterior in position. Loss of one flagellum in *R. simulans*, for instance, would make the zoospore anteriorly uniflagellate.

The other four families to be considered, namely, the Ectrogellaceae, Olpidiopsidaceae, Sirolpidiaceae, and Lagenidiaceae, appear to be more closely related as a whole and constitute an ascending or descending line, depending on which viewpoint one holds. The principal genera of these families con-

## SAPROLEGNIINEEN-PERONOSPORINEEN-SERIES

ZOOSPORES BICILIATE, DIPLANETIC. OOSPORES TYPICALLY DEVELOPED IN OOGONIA. CELLULOSE TYPICAL.

## SAPROLEGNIINAE

CENTRAL SAP VACUOLE. ZOOSPORES FORMED BY AGGREGATION AT THE PERIPHERY. GERMINATION IN TUBE OR SPORANGIUM SEDIMENTATION TUBE CONDENSATION LACKING.

SAPROLEGNIACEAE  
FIRST SWARM STAGE PRESENT  
OP REDUCED ACHLORA-TYPE  
PREDOMINANTLY PARtheno-  
GENESIS ALMOST EXCLUSIVELY  
WITH SEVERAL EGGS NO PERIPLASM

## APHANOMYCOPSIS

ZOOSPORES DIPLANETIC ACHLORA-TYPE SEVERAL ASERIALLY FORMED RESTING SPores OF THE SAPROLEGNIACEAE-TYPE IN A PRUDENTIAL OOGONIUM

## ECTROGELLA

CENTRAL SAP CAVITY. ZOOSPORES FORMED BY AGGREGATION AT THE PERIPHERY. SEVERAL EXIT CANALS. ZOOSPORES DIPLANETIC (ENSTING WITH TWO EQUAL RESTING SPores SOLELY FORMED IN ECTROGELLA)

## AMYLOPHAGUS

SAP VACUOLES DISTRIBUTED FOOD VACUOLES PASSING OVER INTO THE ZOOSPORE PLUMES. ZOOSPORES WITH TWO UNEQUAL CELIA. ONE RESTING SPore PER CYST.

## PROTOMONAS AMYL

FORMING A PLASMODIUM

## PSUEDOSPOROPSIS

ZOOPORES WITH 2 UNEQUAL CELIA

## WORONINA GLOMERATA

AMOEBOID, NAKED PROTOPLAST

## PYTHIUM-PERONOSPORINEAE

FIRST SWARM STAGE LACKING (SUPPRESSED) PYTHIUM-TYPE AND DIRECT DEVELOPMENT OF SECONDARY SWARMS PREDOMINATING TUBE GERMINATION ABUNDANT CONIDA FERTILIZATION OOGONIUM WITH ONE EGG PERIPLASM

PYTHIOGETON  
NO ZOOSPORE NO PERIPLASM

ANCYLISTINEAE  
PYTHIUM-TYPE PREDOMINANT FERTILIZATION TYPICAL NO PREFORMED OOSPORE NO PERIPLASM

OLPIDIOPSIS OEGODONIORUM  
PYTHIUM AND ACHLORA-TYPE OOSPORE NOT FILLING OOGONIUM NO PERIPLASM

## OLPIDIOPSIS

(O SCHENKIANA AS THE TYPE)  
CENTRAL SAP VACUOLE ZOOSPORES BICILIATE, DIPLANETIC WITHOUT ENSTING, DIRECTLY TRANSFORMED AN OOSPORE SEXUALLY FORMED

## PODOPROCTA (ECTOBIELLA) PLATEAU

NO RECEPTION OF FORMED FOODS (?) EXTRANEous FOOD RESERVE PRESENT!

ZOOPORES WITH TWO EQUAL CELIA

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that the four genera and approximately nine species which comprise this family are too poorly known to warrant definite conclusions for the present. As has been pointed out earlier, the type genus *Ectrogella* was formerly included in the chytrid family, Olpidiaceae, by Fischer ('92), Schroeter ('97), Petersen ('05), Minden ('11), Gwynne-Vaughan and Barnes ('26, '37), Fitzpatrick ('30), and others, although Zopf ('84) emphasized its similarities to the Lagenidiaceae (Aenyclisteen). Scherffel's ('25) discovery that the zoospores are biflagellate and diplanetic necessitated the removal of this genus from the chytrids, and he accordingly made it the basis of a new family.

The shape and size of the thallus offer no definite suggestions about to the origin of the Ectrogellaceae because it may be oval, spherical, ellipsoid, or elongate, as in many of the other families. Nevertheless, the grayish granular appearance of the protoplasm, the presence in mature sporangia of a large central vacuole surrounded by a parietal layer of protoplasm, the method of cleavage or zoospore delimitation (*ballung*), and the subsequent occurrence of the homogeneous stage following cleavage indicate direct relationship with the Saprolegniaceae, according to Scherffel. While such characters alone are not always indicative of close affinity, they are supported in this case by the diplanetic behavior of the zoospores. As Scherffel has shown in *Ectrogella*, the primary swarmers are usually apically biflagellate and isocont and swim directly away for a brief period before encysting as in *Saprolegnia*, or they may be aflagellate, glide out, and encyst in a cluster at the mouth of the exit tube as in *Achlya*. The secondary swarmers in *Ectrogella* are lemon-shaped and pyriform, usually with a ventral groove, laterally biflagellate and heterocont with the shorter and more active flagellum extending forward in swimming. In the genus *Eurychasma* the primary swarmers may encyst around the inner periphery of the sporangium as in *Dictyuchus*, but the secondary zoospores do not emerge through individual pores in the sporangium wall as in the latter genus. Instead, they emerge from the cysts into the central portion of the sporangium and then swim out through the exit tube. In *Eurychasmidium* and *Aphanomyopsis* the primary zoospores are reported to behave like those of *Achlya* and *Aphanomyces*. Secondary zoospores, however, have not been observed in *Eurychasmidium*.

Thus, in the family Ectrogellaceae the zoospores may exhibit striking similarities in behavior and structure to those of *Saprolegnia*, *Achlya*, *Aphanomyces* and *Dictyuchus*. Furthermore, in *Ectrogella*, *Aphanomyopsis*, and *Eurychasma* may be found the same degree of reduction of the primary swarming period as occurs from *Saprolegnia* through *Achlya* and *Aphanomyces* to *Dictyuchus*. Whether, on these grounds, the members of the Ectrogellaceae are to be considered primitive or reduced and degenerate saprolegniaceous species is not clearly evident. Mycologists who adhere to the reduction hypothesis

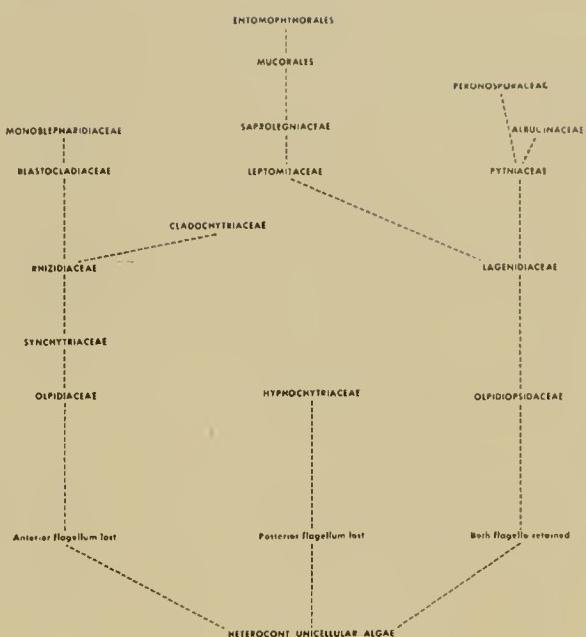


DIAGRAM 2. Phylogeny of the Phycomycetes based upon the theory of their origin from unicellular algae. After Bessey 1942.

may well argue that the thallus of this family has undergone reduction while the zoospores have retained their diplanetic behavior. Scherffel, however, regarded them as primitive and held that the type of diplanetism exhibited is derived from the Proteomyxa or Monadineae instead of the Saprolegniales. In line with his belief that the Phycomycetes in general are derived from the Monadineae as shown in diagram 1, he accordingly concluded that *Ectrogella* and *Aphanomyopsis* may have originated from biflagellate heterocont genera similar to *Aphelidiopsis*, *Pseudosporopsis*, and *Amylophagus* and possibly inherited their diplanetic habit from an ancestor like *Pseudospora leptoderma*. He also believed that the large central sap cavity or vacuole present in zoosporangia is a relic of a proteomyxean ancestor.

On the basis of the type of sexual reproduction Scherffel further believed that *Ectrogella* may be connected on one hand with the Saprolegniaceae and Leptomitaceae through *Aphanomyopsis* and on the other hand with the Peronosporaceae through *Olpidiopsis*, the Lagenidiaceae, and *Pythiogoton*. However, as has been emphasized before, the occurrence of sexual reproduction in the Ectrogellaceae has not been conclusively proven. Resting spores are known in only three species. In *E. perforans* they appear to be nothing more than vegetative thalli which have encysted and developed thick walls. Scherffel regarded the resting spore of *E. Licmophorae* as an oospore in a rudimentary oogonium, although he did not actually observe sexual fusion. As the present author has already pointed out, this resting spore may possibly be nothing more than the

contracted and encysted content of an irregular, lobed thallus. In *Aphanomyopsis bacillariacearum* one or more asexual resting spores are formed in a thallus or a segment thereof, and Scherffel accepted this as an indication of even closer relation to the Saprolegniaceae. Obviously much more study on the occurrence of sexuality in this family is essential before this character can be used as a basis of comparing relationships. Nevertheless, Scherffel's belief that there is a close affinity between the Ectrogellaceae and the Saprolegniaceae has been rather widely accepted, although subsequent workers have not been certain about whether the former family represents an ascending or descending series in the evolution of the Phycomycetes. Gaumann ('26), Gaumann and Dodge ('28) included *Eurychasma* and *Ectrogella* in the Acanthostichaceae (Lagenidiaceae) and emphasized their close relationship to *Lagenidium*, *Myzocytium*, and the Saprolegniaceae. Sparrow ('33, '36) included *Ectrogella* and *Aphanomyopsis* in the Saprolegniales without committing them to any particular family, but in 1942 he placed them in the Ectrogellaceae and made this family the first and most primitive of the Saprolegniales. Coker and Matthews ('37) also included the Ectrogellaceae in this order next to the Saprolegniaceae.

Very little can be said about the origin and relationships of the Sirolpidiaceae at present, because this family is even less known than the Ectrogellaceae. It has no particularly outstanding family characteristics which relate it distinctly to any of the other groups. The genera *Sirolpidium* and *Pontisma* were formerly included by Petersen ('05) in the Holochytriaceae of the Mycochytridiales, although he had discovered that the zoospores of the type species, *S. Bryopsidis*, are biflagellate and not chytrid-like. His findings were confirmed by Sparrow ('34, '36) who later ('42) proposed the family Sirolpidiaceae for these genera and placed it in the Lagenidiales between the Olpidiopsidaceae and Lagenidiaceae. Whether or not present-day knowledge warrants this position is obviously open to question, but the nature of the vegetative thallus of the Sirolpidiaceae nevertheless suggests such a relationship. The thallus has a tendency to become elongate, filamentous, and somewhat mycelioid and may fragment into sections like those of some species of *Lagenidium* and *Myzocytium*. On the other hand, the thallus may sometimes be unicellular and olpidioid like those of the Olpidiopsidaceae. These likenesses are also correlated with similarities in the general appearance of the protoplasm, the presence of a large central vacuole bounded by a parietal layer of protoplasm in the mature zoosporangium before cleavage, and the method of cleavage. Size, shape, and structure of the thallus, however, are vegetative characters which vary markedly and by themselves are not always significant phylogenetically, so that too much emphasis must not be placed on them.

So far as is now known the zoospores are not diplanetic, and in this respect do not show affinity with the Ectrogellaceae or the diplanetic members of the Lagenidiaceae. According to Sparrow ('34), the zoospores of *S. lagenidioides* are strikingly similar in behavior and appearance to those of *Rozellopsis inflata*, while in *Petersenia lobata* the late cleavage and early zoospore stages resemble those of *Pythium*. Thus, aside from their arched, pyriform or slightly reinform shape and the presence of two flagella the zoospores offer few clews to the relationship of the Sirolpidiaceae. Comparisons on the basis of type of sexual reproduction cannot be made because nothing is known about sexuality in this family. Resting spores are unknown in most species, and in those for which they have been reported they appear to be nothing more than vegetative thalli which have encysted and become thick-walled.

Most species of the family Olpidiopsidaceae are fully known as to life cycles and development, and the indications of relationship are accordingly more clearly defined. In thallus structure and appearance all species show a striking parallelism to the olpidiaceous chytrids, and for this reason they were first included in the Olpidiaceae and later in the Pseudolpidiaceae and Woroninaceae by most mycologists and designated as biflagellate chytrids. This close resemblance in vegetative structure is probably due to convergent evolution and may not be indicative of affinity. Sharply defined diplanetism does not occur in this family except in *Olpidiopsis Oedogoniorum* and *Pythiella vernalis*—two species which possibly do not belong in the Olpidiopsidaceae. In most species of *Olpidiopsis*, however, the zoospores may come to rest, retract their flagella, become amoeboid, and then remain quiescent for a while, but they do not encyst. After a short while flagella are formed again, and the zoospores resume their motility. The insertion and position of the flagella appear to be the same during both motile periods. Butler ('07) compared this interruption of motility to diplanetism in the Saprolegniaceae, and later Scherffel ('25) described it as diplanetism without encystment. Whether or not the behavior of these zoospores is to be regarded as evidence of primitive and rudimentary diplanetism which foreshadows the development of true diplanetism in the Ectrogellaceae, Lagenidiaceae, and Saprolegniaceae is, of course, a debatable question. In *O. Oedogoniorum*, as noted before, true diplanetism has been reported by Scherffel, but the primary swarming period may be reduced to nothing more than the emergence of the zoospores and a slight beating of the flagella. Occasionally the entire content of the sporangium may emerge as a protoplasmic mass and then undergo cleavage into zoospores on the outside as in *Lagenidium* and *Pythium*. A similar behavior was occasionally noted by Coker ('23) in *O. Saprolegniae*. In *P. vernalis* the primary swimmers are aflagellate and merely glide out of the exit tube, near the mouth of which they encyst. The behavior of the zoospores in these three species ranges from that of

*Achlya* to *Lagenidium* and *Pythium*. As noted before, however, *O. Oedogoniorum* may possibly be a species of *Lagenidium* while *P. vernalis* may relate to another family. In these events, the occurrence of true diplanetism in the Olpidiopsidaceae remains to be conclusively demonstrated. So far nothing is known of its occurrence in *Pseudosphaerita* and *Blastulidiopsis*. The flagella of *Olpidiopsis*, particularly of *O. Saprolegniae*, are structurally similar to those of the Lagenidiaceae. Saprolegniales and Peronosporales, according to Conch ('41). One of the flagella bears hairs or tinsels, while the other is of the whip lash type.

Except for *Pseudosphaerita*, which is a doubtful member of this family, the appearance of the vacuolate protoplasm and the method of zoosporogenesis of most species are very similar to those of the reduced members of the Lagenidiaceae, and unless the type of sexual reproduction is observed it is difficult and almost impossible to tell the species apart. On these grounds then the Olpidiopsidaceae and Lagenidiaceae appear to be directly related.

To many mycologists the type of sexual reproduction exhibited by the Olpidiopsidaceae is primitive and indicates an even closer relationship to the Lagenidiaceae. In *Olpidiopsis* the degree of sexuality varies considerably in the same and in different species, and sex does not appear to be well established for the genus as a whole. The resting spores (oospores?) in some species are entirely asexual or parthenogenetic and appear to be nothing more than encysted, thick-walled vegetative thalli, while in other species, *O. Achlyae*, for example, 75 per cent of them may be parthenogenetic and the remainder zygotic. At the other extreme are species in which the spores are 100 per cent zygotic. Further evidence of variability in degree of sexuality is shown by some partially parthenogenetic species in which only a portion of the male gamete fuses with the female. Also, one male gamete may occasionally "serve" two females, or one female may be fertilized by two to eight male gametes. Furthermore, except for size differences, the gametes are not markedly differentiated as such. Structurally, they do not appear to be very different from ordinary vegetative thalli or sporangia and are morphologically equivalent to these structures. The male thallus is usually smaller than the female, but occasionally the two are equal in size. Sexual reproduction in the Olpidiopsidaceae is, nevertheless, predominantly heterogamous. However, no egg cell or oospore is differentiated in the so-called oogonium in preparation for fusion, and except for the questionable species, *O. Oedogoniorum*, the oospore completely fills the thallus in which it develops. The type of undifferentiated gametes together with the great variability in degree of sexual expression in *Olpidiopsis* suggest very strongly that this genus and other members of the Olpidiopsidaceae are primitive, but on the other hand they may equally well indicate reduction and degeneration. Nonetheless, Barrett, Cavers, Scherffel, Cook, and others regarded *Olpidiopsis* as primitive.

Cavers and Cook derived it from the Olpidiopsidaceae in the Chytridiales, but Scherffel believed that it originated from an *Ectrogella*-like ancestor (diagram 1). He regarded *O. Schenkiana* as representative of the genus as a whole, and from such species evolution proceeded along the line of *O. Oedogoniorum* to the Ancylistineae (Lagenidiaceae). The last named species, according to him, is very significant phylogenetically, since the oospore lies free in a vesicle or rudimentary oogonium and is difficult to distinguish from species of *Lagenidium*, particularly *L. Oedogonii*. In *Pythiella vernalis* sexual reproduction resembles that of *O. schenkiana* but differs from that of *Olpidiopsis* in general and the Lagenidiaceae by the partial differentiation of an egg cell in the oogonium and the presence of a small amount of periplasm. By these characters *P. vernalis* resembles species of *Pythium* with which it may possibly be closely related. Scherffel's interpretation of the relationships of *Olpidiopsis* and related genera has been followed very closely by Sparrow ('42) and Bessey ('42). Sparrow, as noted before, included the Olpidiopsidaceae in the Lagenidiales.

The Lagenidiaceae is the most complex group of the holobiflagellomycetes and is generally regarded as the climax family. Due largely to the fact that many of the species are incompletely known, this family has undergone the usual vicissitudes of classification and in mycological literature may be found in various relations to the Archimycetes and higher Oomycetes. The similarities of *Myzocytium* and *Lagenidium* to reduced specimens of *Pythium* were so striking that Schenk ('59), Pringsheim ('58), and Walz ('70) at first included the type species of these genera in *Pythium*. Since that time a great many mycologists have recognized this close resemblance to the Pythiaceae and included the Lagenidiaceae among the higher Oomycetes, but as in the case of the other families previously discussed these workers were not in agreement whether this family represents an ascending or degenerating line. The viewpoints of many workers were influenced by the generally held belief that *Ancylistes* and other similar non-zoosporic genera, were closely related to the Lagenidiaceae. Had they known that *Ancylistes* and probably other genera also are members of the Entomophthorales, their interpretations would doubtless have been different. The fact that their viewpoints provided for *Ancylistes* must be borne in mind relative to any criticisms which are made below.

De Bary ('84), Schroeter ('86), Tavel ('92), Butler ('07), Clements ('09), Scherffel ('25), Clements and Shear ('31), Wettstein ('35), Sparrow ('36, '42), and others included the Lagenidiaceae (Ancylistaceae) among the Oomycetes in close relation to the Pythiaceae and Peronosporaceae, but Bessey ('37) and Coker and Matthews ('37) regarded it as a family of the Saprolegniales. Gaumann ('25) and Gaumann and Dodge ('28) also included the Lagenidiaceae in the Oomycetes but discussed it as a family between the Blastocladiaceae and Saprolegniaceae. De Bary and Tavel

were of the opinion that it embraces only reduced and degenerate species which have arisen as the result of submersed parasitism—a viewpoint which has been revived by Gaumann, Gaumann and Dodge, and Mez. However, the majority of students of this group, including Schroeter ('97), Minden ('11), Atkinson ('09), Cavers ('15), Scherffel ('25), Cook ('28), and Fitzpatrick ('30), believed that this family constitutes an ascending series which has given rise to various groups of the Phycomycetes. Atkinson related *Lagenidium* to the chytrid *Polyphagus* and postulated that the Lagenidiaceae may have originated from certain species of the Rhizidiaceae and in turn led to the development along more or less parallel lines to the higher Oomycetes and Zygomycetes. In this connection it may be noted that many years earlier Zopf ('84, p. 190) suggested that *Rhizidiomyces apophysatus* may be a type of species which relate the Rhizidiaceae with the Acanthostichaceae (Lagenidiaceae) and Pythiaceae. While Cavers believed that the Phycomycetes originated in the Proteomyxa, he thought that the Acanthostichaceae (Lagenidiaceae) are derived from the Chytridiales and lead to the Peronosporaceae. Scherffel, as noted before, believed that the Lagenidiaceae developed from *Ectrogella*- and *Olpidiopsis*-like ancestors and is connected with his *Pythium*-Peronosporales series through *Pythiogeton* (diagram 1). *Lagenidium Cyclotellae*, in his opinion, is a connecting link between *Ectrogella* and the Lagenidiaceae (Acanthostichaceae). Cook regarded the Acanthostichaceae (Lagenidiaceae) as intermediate between the Chytridiales and Oomycetes proper and believed that it may have given rise on one hand to the Saprolegniaceae through the Blastocladiales and Leptomitaceae, and on the other hand to the Peronosporaceae through the Pythiaceae and Albuginaceae (diagram 3). Inasmuch as the

Present day evidence indicates that the Blastocladiales may have originated directly from the Chytridiales. Sparrow ('42) placed the Lagenidiaceae at the top of the Lagenidiales next to the Peronosporales, suggesting thereby that it may have originated from the Olpidiopsidaceae and Siroplidiaceae. Bessey ('42) likewise derived it from the Olpidiopsidaceae and suggested (diagram 2) that it may have given rise in a more or less direct line to the Pythiaceae, Albuginaceae and Peronosporaceae on one hand and to the Leptomitaceae and Saprolegniaceae on the other.

Having reviewed briefly the various views on the phylogeny of the Lagenidiaceae, let us now examine the data on which they are based. In size and shape the thallus of some species of this family resembles the mycelium of the filamentous Oomycetes, but in other species it is like that of the Olpidiopsidaceae. These characters, therefore, do not always afford a fundamental basis of relationship. Fischer and Lottsy, nevertheless, used them and the holocarpic nature of the thallus as the chief grounds for including the Lagenidiaceae in the sub-order Mycochytridinae, following the Olpidiaceae and Syncytriaaceae. At that time few species with extensive, filamentous, mycelioid thalli were known so that the oval, ellipsoid or tubular, irregular, vermiform and elongate shapes were regarded as more characteristic of the family. Since then species like *Lagenidium marchalianum*, *L. Closterii*, *L. giganteum*, etc., have been described, the thalli of which can hardly be distinguished from the mycelium of *Pythium*. Conversely, reduced, holocarpic, relatively short, vermiform and unbranched thalli may rarely occur in *Pythium*, *Achlya*, etc., so it is obvious that within certain limits size, shape, and extent of thallus are not always of fundamental value in judging affinity.

In methods of zoosporegenesis and the behavior of the zoospores after emerging, several lines of relationship are suggested. The majority of species show distinct pythiacous tendencies because the primary swarm period is suppressed and lacking. The protoplasm emerges from the sporangium and undergoes cleavage on the outside with or without a surrounding vesicular membrane. *Lagenidium Oedogonii* and *Lagenidium* sp. Couch, on the other hand, exhibit a combination of *Pythium*, *Saprolegnia* and *Achlya* characteristics. In the former species the zoospores may be formed extramatrically in a vesicle as in *Pythium* or within the sporangium and then encyst at the mouth of the exit tube after emerging as in *Achlya*. In the latter species they are formed in a vesicle but after swimming about for a short while they encyst. Within one to three hours, they emerge from the cysts and become motile again as in *Saprolegnia*. In *L. Cyclotellae*, however, the zoospores are formed in the same manner and behave like those of *Olpidiopsis* and some species of *Ectrogella*.

In shape, structure, position of the flagella, and type of swimming the zoospores of most species are essentially like those of *Pythium* and the secondary

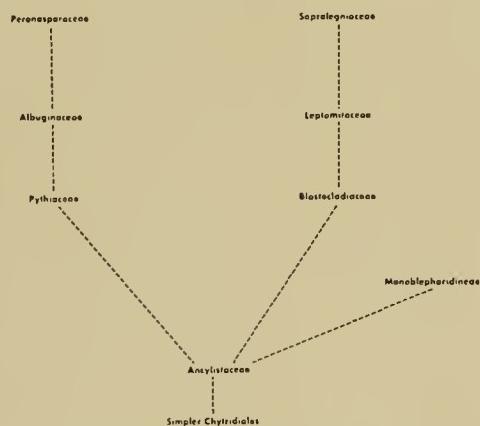


DIAGRAM 3. The origin of the Acanthostichaceae (Lagenidiaceae) and its relation to the higher Oomycetes, according to Cook, 1928.

zoospores of the Blastocladiales are uniflagellate and both gametes are motile, it is difficult to conceive how this order has arisen from the Lagenidiaceae.

swarmers of *Saprolegnia* and other related genera. In *L. Cyclotellae*, however, they are more similar to those of *Ectrogella*, while the markedly heterocont zoospores of *L. enecans* and *Myzocytium*, described by Scherffel ('25) and Dangeard ('06) are somewhat like those of *O. Ricciae*, *O. irregularis*, *Pseudolpidium Glenodineanum*, *P. Sphaerita*, and *Pseudosphaerita*. Additional evidence of relationship between the Lagenidiaceae, Olpidiopsidaceae, Saprolegniaceae and Peronosporaceae is suggested by the fact that the zoospores of *Resticularia* and *Myzocytium* and probably other genera have one tinsel and one whip lash type of flagellum.

In sexual reproduction some species of the Lagenidiaceae may perhaps show a slight advance over that exhibited by the Olpidiopsidaceae by the fact that the oospore lies free in the oogonium and the gametangia are slightly more differentiated. In species of *Lagenidium* the oogonium is usually larger, more vesicular and frequently barrel-shaped, while the antheridium is tubular and elongate. In *L. enecans*, for example, the antheridium may be closely applied to the oogonium as in the Saprolegniaceae, according to Scherffel. In other genera like *Myzocytium*, *Lagena* and *Resticularia*, however, the gametangia are less differentiated and often appear to be nothing more than potential sporangia, with which they are morphologically equivalent. In no genus is an egg cell differentiated in the oogonium in preparation for plasmogamy, nor is periplasm present. In both of these respects the Lagenidiaceae differ from most of the Peronosporales, but show some resemblance to the Saprolegniaceae by the absence of periplasm. The contraction of the ooplasm during plasmogamy in *L. rabenhorstii* may perhaps foreshadow a tendency toward differentiation of an egg cell before fertilization. That some differentiation does occur in the oogonium and antheridium is suggested by Dangeard's report that the supernumerary nuclei in *M. vermiculatum* degenerate and only one from each gametangium functions in karyogamy as in species of the Peronosporales. Only one species of the Lagenidiaceae has been studied cytologically in this respect, and whether or not this type of nuclear behavior is characteristic of the family as a whole remains to be seen. The so-called oospores are nevertheless similar in appearance and structure to those of the Saprolegniales as well as the resting spores of many chytrids and species of the Proteomyxa.

Since the gametangia and gametes are not highly differentiated, Atkinson, Barrett, Cook, and others regarded sexual reproduction in the Lagenidiaceae as a generalized oomycetous type with tendencies in more than one direction. Atkinson in particular emphasized the isogamous and zygomycetous potentialities and their relation to the origin of the Zygomycetes from this family. As noted previously, sexual reproduction in *Resticularia*, *Lagena*, and *Lagenidium sacculoides* is isogamous, which lends support to the hypothesis that the Zygomycetes also may have originated from lagenidiaceous ancestors.

It is apparent from this discussion of origin and relationships that the so-called holobitflagellomycetes have some characteristics in common with the Proteomyxa, Plasmodiophorales, Chytridiales, Saprolegniales, Peronosporales, and Zygomycetes. As to their origin, three principal theories have been proposed: (1) that they are reduced and degenerate oomycetes resulting primarily from submersed parasitism; (2) that they have been derived from heterocont unicellular algae through the loss of chlorophyll and the assumption of a parasitic mode of life, and (3) that they have originated from simpler fungi like the Chytridiales or the more primitive Proteomyxa. Their resemblance to the Chytridiales apparently is due more to parallelism of development or convergent evolution than close relationships. The genera included in the provisional family Woroninaeae show varying degrees of similarity to certain proteomyxean species and the Plasmodiophorales by their mode of nutrition and the presence of plasmodia and sori. The remaining families, on the other hand, exhibit marked Oomycete relationships by their diplanetous zoospores and predominantly heterogamous type of sexual reproduction. These affinities involve principally the Saprolegniales and Peronosporales.

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## Chapter VIII

### Hosts and Bibliography

THE FUNGI described in the previous chapters are widely distributed in nature and ubiquitous in host range. As noted before, they occur in fungi, freshwater and marine algae, liverworts, mosses, gymnosperms, angiosperms, infusoria, rotifers, nematodes, insects, and erustaceans. With the view of expediting reference to these fungi and their hosts, a complete host index and bibliography is herewith presented. The hosts are listed in solid type and their parasites in italics. The arrangement of the divisions, orders, and families of hosts does not follow any particular system of classification. Systematists in particular fields will doubtless object to and take issue with the present arrangement, but the primary object of this index is not a classification of algae, fungi, higher plants, and animals. In order to avoid confusion through personal interpretation of synonymy, the hosts as well as their parasites are listed in the same manner as reported by the various workers. The exact identity of many of the early described parasites is doubtful. The early workers were not very specific in their reports and descriptions, so that it is not certain which species of *Olpidiopsis*, *Myzocyltum*, *Lagenidium*, etc., Nägeli, Cienkowski, Stein, Pringsheim, Reinsch and others, for example, referred to. Such parasites have, nevertheless, been listed with question marks in the index with the view of bringing them to the notice of research workers.

### THALLOPHYTA

#### FUNGI

##### *Olpidiaceae*

###### *Sphaerita endogena*

###### *Olpidium Sphaeritae*

Dangeard, 1889. Le Bot. 1: 51.

###### *Pseudotolidium Sphaeritae* (Dang.)

Fischer, 1892. Rabenhorst's Krypt'fl. I, 4: 36.

###### *Olpidiopsis Sphaeritae* (Dang.)

Schroeter, 1897. Engler und Prantl, Die Nat. Pflanzf. I, 1: 69.

###### *Rozella septigena*

###### *Olpidiopsis irregularis* (?)

Constantineanu, 1901. Rev. Gen. Bot. 13: 376.

###### *Saprolegniaceae*

###### *Achlya* sp.

###### *Woronina polycystis*

Dangeard, 1890. Le Bot. 2: 145.

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###### *Rozella simulans*

Maurizio, 1895. Jahrb. Nat. Gesell. Graubündens 38: 9.

###### *Rozellopsis simulans* (Fischer)

Karling, 1942. Amer. Jour. Bot. 29: 33. 1942, Mycologia 34: 207.

###### *Olpidiopsis incrassata*

Sorokin, 1883. Arch. Bot. Nord France 2: 29. 1889, Rev. Mycol. 11: 84.

###### *Pseudotolidium incrassata*

Sparrow, 1933. Mycologia 25: 515.

###### *Olpidiopsis Suproleguae*

Petersen, 1909. Bot. Tidsskr. 29: 404. 1910, Ann. Mycol. 8: 539.

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Cornu, 1872. Ann. Sci. Nat. 5 ser. 15: 147.

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###### *Pseudotolidium fusiforme*

Sparrow, 1932. Mycologia 24: 272. 1936, Jour. Linn. Soc. London, Bot. 50: 425.

###### *Olpidiopsis index*

Cornu, 1872, l.c. p. 145.

###### *Achlya americana*

###### *Woronina* (?) *asterina*

Tokunaga, 1933. Trans. Sapporo Nat. Hist. Soc. 13: 26.

###### *Achlya colorata*

###### *Olpidiopsis varians*

Shanor, 1940. Jour. Elisha Mitchell Sci. Soc. 56: 171.

- Achlya de Baryana*  
*Woronina polycystis*  
 Cook and Nicholson, 1933, Ann. Bot. 47: 857.
- Achlya flagellata*  
*Rozella simulans*  
 Tokunaga, 1933, Trans. Sapporo Nat. Hist. Soc. 13: 25.  
*Rozellopsis simulans* (Fischer)  
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- Olpidiopsis Saprolegniae*  
 Coker, 1923, The Saprolegniaceae, p. 184.
- Olpidiopsis fusiformis* (?)  
 Cienkowski, 1855, Bot. Zeit. 13: 801.
- Olpidiopsis minor*  
 Matthews, 1935, Jour. Elisha Mitchell Sci. Soc. 51: 310.
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- Achlya imperfecta*  
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- Olpidiopsis fusiformis*  
 Shanor, 1940, Jour. Elisha Mitchell Sci. Soc. 56: 171.
- Achlya klebsiana*  
*Olpidiopsis fusiformis*  
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- Achlya leucosperma*  
*Olpidiopsis fusiformis*  
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 Fischer, 1892, Rabenhorst's Krypt'fl. I, 4: 36.
- Olpidiopsis minor*  
 Fischer, 1892, l.c., p. 39.
- Achlya polyandra*  
*Woronina polycystis*  
 Cormu, 1872, Ann. Sci. Nat. 5 ser. 15: 177.
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 Fischer, 1882, Jahrb. Wiss. Bot. 13: 321.
- Rozellopsis simulans* (Fischer)  
 Karling, 1942, Amer. Jour. Bot. 29: 33, 1942, Mycologia 34: 207.
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 Fischer, 1882, Jahrb. Wiss. Bot. 13: 364.
- Pseudolpidium fusiforme*  
 Fischer, 1892, Rabenhorst's Krypt'fl. I, 4: 36.
- Achlya proliferoides*  
*Olpidiopsis varians*  
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*Olpidiopsis Saprolegnia*  
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- Isoachlya eccentrica*  
*Olpidiopsis Saprolegniae*  
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*Olpidiopsis Saprolegniae*  
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*Olpidiopsis echinata*  
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*Olpidiopsis Saprolegniæ*  
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*Woronina polycystis*  
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*Maurizio*, 1895, Jahrb. Nat. Gesell. Graubündens  
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*Dangeard*, 1890, Le Bot. 2: 63.
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*Pythiella vernalis*  
*Couch*, 1935, Mycologia 27: 160.
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*Butler*, 1907, Mem. Dept. Agr. India 1, no. 5: 126, 127.
- Rozellopsis inflata* (Butler)  
*Karling*, 1912, Amer. Jour. Bot. 29: 34, 1942, Mycologia 34: 205.
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*Butler*, 1907, i.e., p. 127.
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*Whiffen*, 1942, Amer. Jour. Bot. 29: 610.
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*Pseudolpidium Pythii*  
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*Tokunaga*, 1933, Trans. Sapporo Nat. Hist. Soc.,  
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*Pseudolpidium Pythii*  
*Butler*, 1907, i.e., p. 127.
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*Karling*, 1912, Amer. Jour. Bot. 29: 34, 1942, Mycologia 34: 206.
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*Pleolpidium* sp.  
*Waterhouse*, 1910, Trans. Brit. Mycol. Soc. 24: 7,  
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- Rozellopsis waterhousei*  
*Karling*, 1912, Amer. Jour. Bot. 29: 34, 1942, Mycologia 34: 206.
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- Pilobolus* sp.  
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- MYXOPHYCEAE**
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*Reticularia nodosa*  
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- Oscillatoriaceae*
- Tolypothrix* sp.  
*Reticularia boudlei*  
*Fritsch*, 1903, Ann. Bot. 17: 651.
- R. nodosa* (?)  
*Fritsch*, 1903, i.e., p. 650.
- HETEROKONTAE**
- Tribonemaceae*
- Tribonema bombycinum*  
*Olpidiopsis sorokinii*  
*De Wildeman*, 1890, Ann. Soc. Belg. Micro. 14: 22.
- Cryptomonadaceae*
- Cryptomonas ovata*  
*Sphaerita radialis*  
*Dangeard*, 1890, Le Bot. 2: 51.
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- Euglena* sp.  
*Myzocytium* sp. (?)  
*Sparrow*, 1936, Jour. Linn. Soc. London Bot. 50: 463.
- Euglena caudata*  
*Pseudosphaerita Euglena*  
*Mitchell*, 1928, Trans. Amer. Micro. Soc. 17: 30.
- Euglena polymorpha*  
*Pseudosphaerita Euglena*  
*Dangeard*, 1895, Le Bot. 4: 213, 1933, Ibid. 25: 36.
- Euglena sanguinea*  
*Pseudosphaerita Euglena* (?)  
*Nägler*, 1911, Arch. Protistk. 23: 263.
- Euglena viridis*  
*Pseudosphaerita Euglena*  
*Dangeard*, 1895, Le Bot. 4: 213, 1933, Ibid. 25: 36.  
*Stein*, 1878, Der Organismus der Infusionsthiere,  
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- Peridiniaceae*
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*Olpidium Glenodinianum*  
*Dangeard*, 1882, Jour. de Bot. 2: 130.
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*Fischer*, 1892, Rabenhorst's Kryptfl. I, 1: 36.
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- Bacillariaceae*
- Amphora ovalis*  
*Lagenidium eucaneans*  
*Scherffel*, 1925, Arch. Protistk. 52: 20.

- Cocconema lanceolatum*  
*Ectrogella bacillariacearum*  
 Gill, 1893. Jour. Roy. Micro. Soc. 1893: 1.
- Lagenidium enecans*  
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*Lagenidium Cyclotellae*  
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- Cymatopleura solea*  
*Lagenidium enecans*  
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- Cymbella cymbiformis* var. *parva*  
*Lagenidium brachystomum*  
 Scherffel, 1925, l.c., p. 21.
- Cymbella gastroides*  
*Aphanomyopsis bacillariacearum*  
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- Lagenidium enecans*  
 Scherffel, 1925, l.c., p. 20.
- Epithemia turgida*  
*Aphanomyopsis bacillariacearum*  
 Scherffel, 1925, l.c., p. 14.
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*Ectrogella bacillariacearum*  
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 De Wildeman, 1896. Ann. Soc. Belge Micro. 20: 41.
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*Lagenidium brachystomum*  
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*Ectrogella Gomphonematis*  
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 Petersen, 1905. Overs. Kgl. Dansk. Vids. Selsk. Forh.  
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*Ectrogella Liemophorae*  
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 Sparrow, 1934. Dansk. Bot. Ark. 8, no. 6: 19.
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*Ectrogella bacillariacearum*  
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 Domjan, 1935. Folio Cryptogam. 2: 9.
- Navicula* sp.  
*Aphanomyopsis bacillariacearum*  
 Tokunaga, 1934. Trans. Sapporo Nat. Hist. Soc. 13:  
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*Lagenidium brachystomum*  
 Scherffel, 1925, l.c., p. 21.
- Nitzschia sigmaoidea*  
*Ectrogella bacillariacearum*  
 Gill, 1903. Jour. Roy. Micro. Soc. 1893: 1.
- Aphanomyopsis bacillariacearum*  
 Scherffel, 1925, l.c., p. 14.
- Pinnularia* sp.  
*Ectrogella bacillariacearum*  
 Zopf, 1884. Nova Acta Ksl. Leop.-Carol. Deut. Akad.  
 Nat. 47: 177.  
 Scherffel, 1925. Arch. Protistk. 52: 6.  
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- Ectrogella monostoma*  
 Sparrow, 1933, l.c., p. 531.
- Aphanomyopsis bacillariacearum*  
 Sparrow, 1933, l.c., p. 530.
- Lagenidium* sp.  
 Scherffel, 1925, l.c., p. 23.
- Pinnularia viridis*  
*Aphanomyopsis bacillariacearum*  
 Scherffel, 1925, l.c., p. 14.
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*Ectrogella bacillariacearum*  
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*Lagenidium enecans*  
 Scherffel, 1925, l.c., p. 20.
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*Ectrogella perforans*  
 Sparrow, 1936. Biol. Bull. 70: 239.
- Surirella* sp.  
*Aphanomyopsis bacillariacearum*  
 Tokunaga, 1934. Trans. Sapporo Nat. Hist. Soc. 13:  
 227.
- Synedra* sp.  
*Ectrogella bacillariacearum*  
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 Nat. 47: 177.  
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 De Wildeman, 1892. Ann. Soc. Belge Micro. 20: 41.
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*Ectrogella bacillariacearum*  
 Zopf, 1884. Nova Acta Ksl. Leop.-Carol. Dent. Akad.  
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- Synedra ulna*  
*Ectrogella perforans*  
 Petersen, 1905. Overs. Kgl. Dansk. Vids. Selsk. Forh.  
 5: 466.
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 Scherffel, 1925. Arch. Protistk. 52: 6.  
 Domjan, 1935. Folio Cryptogam. 2: 9.
- Ectrogella monostoma*  
 Scherffel, 1925, l.c., p. 8.

## CHLOROPHYCEAE

## Chlamydomonadaceae

Chlamydomonas alboviridis

*Pseudosphaerita Euglenae* (?)

Stein, 1878, Der Organismus der Infusionsthiere, Abt. III, pl. 14, fig. VI 4-11.

Chlamydomonas pulvisculus

*Pseudosphaerita Euglenae* (?)

Stein, 1878, l.c., pl. 15, fig. 36.

## Zygneaceae

Mesocarpus sp.

*Olpidiopsis schenkiana*

Zopf, 1881, Nova Acta Ksl. Leop.-Carol. Deut. Akad. Nat. 47: 168.

*Diplophysa schenkiana*

Schroeter, 1897, Engler und Prantl, Die Nat. Pflanz'f. I, 1: 85.

*Pseudolpidiopsis schenkiana*

Minden, 1911, Krypt'fl. Mark Brandenburg 5: 257.

*Diplophysa elliptica*

Schroeter, 1886, Cohn's Krypt'fl. Schlesiens 3: 196.

*Olpidiopsis elliptica*

Fischer, 1892, Rabenhorst's Krypt'fl. I, 4: 41.

*Pseudolpidiopsis elliptica*

Minden, 1911, Krypt'fl. Mark Brandenburg 5: 260.

*Olpidiopsis appendiculata*

De Wildeman, 1895, La Notarisia 10: 34. 1896, Ann. Soc. Belge Micro. 20: 29.

*Pseudolpidiopsis appendiculata*

Minden, 1911, Krypt'fl. Mark Brandenburg 5: 259.

*Lagenidium rabenhorstii*

Zopf, 1878, Verh. Bot. Ver. Prov. Brandenburg 20: 79. 1881, Nova Acta Ksl. Leop.-Carol. Deut. Akad. Nat. 47: 145.

*Myzocytium proliferum*

Zopf, 1881, l.c., p. 159.

Scherffel, 1902, Nov. Közl. 1: (109). 1926, Arch. Protistk. 54: 245.

*M. irregulare*

Cejp, 1935, Bull. Int. l'Acad. Sci. Bohême 1935: 7.

Mesocarpus pleurocarpus

*Myzocytium proliferum*

Schroeter, 1886, Cohn's Krypt'fl. Schlesiens 3: 227.

Mougeotia sp.

*Olpidiopsis schenkiana*

Zopf, 1881, Nova Acta Ksl. Leop.-Carol. Deut. Akad. Nat. 47: 168.

*Lagenidium rabenhorstii*

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Valkanov, 1931, Arch. Protistk. 73: 365.

*Myzocytium proliferum*

Schenk, 1858, Über das Vorkommen Contractiler Zellen im Pflanzenreich, p. 10.

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*M. irregulare*

Cejp, 1935, Bull. Int. l'Acad. Sci. Bohême 1935: 7.

Spirogyra sp.

*Olpidiopsis schenkiana*

Zopf, 1881, Nova Acta Ksl. Leop.-Carol. Deut. Akad. Nat. 47: 168.

De Wildeman, 1890, Ann. Soc. Belge Micro. 11: 24. 1891, Bull. Soc. Roy. Bot. Belg. 30: 172. 1896, Ann. Soc. Belge Micro. 20: 28.

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Butler, 1907, Mem. Dept. Agr. India 1, no. 5: 135.

Buller and Bisby, 1931, Fungi of India.

Scherffel, 1925, Arch. Protistk. 52: 138.

*Pleocystidium parasiticum*

Fisch, 1881, Sitzb. Phys.-Med. Soc. Erlangen 16: 60.

*Olpidiopsis parasitica* (Fisch.)

Fischer, 1892, Rabenhorst Krypt'fl. I, 4: 40.

*Diplophysa schenkiana* (Zopf)

Schroeter, 1897, Engler und Prantl, Die Nat. Pflanzen'f. I, 1: 85.

*Pseudolpidiopsis schenkiana* (Zopf)

Minden, 1911, Krypt'fl. Mark Brandenburg 5: 257.

Tokunaga, 1933, Trans. Sapporo Nat. Hist. Soc. 13: 82.

*P. parasitica* (Fisch.)

Minden, 1911, l.c., p. 258.

*Olpidiopsis zopfi*

De Wildeman, 1895, La Notarisia 10: 34. 1896, Ann. Soc. Belge Micro. 20: 25.

*Pseudolpidiopsis zoppii* (de Wildeman)

Minden, 1911, Krypt'fl. Mark Brandenburg 5: 259.

*Olpidiopsis fibrillosa*

De Wildeman, 1895, La Notarisia 10: 34. 1896, Ann. Soc. Belge Micro. 20: 27.

*Pseudolpidiopsis fibrillosa*

Minden, 1911, Krypt'fl. Mark Brandenburg 5: 259.

*Lagenidium rabenhorstii*

Zopf, 1878, Verh. Bot. Ver. Prov. Brandenburg 30: 79. 1879, Hedwigia 18: 94. 1884, Nova Acta Ksl. Leop.-Carol. Deut. Akad. Nat. 47: 145.

De Wildeman, 1891, Bull. Soc. Roy. Bot. Belg. 30: 137. 1893, Ann. Soc. Belge Micro. 17: 45. 1895, Mem. Soc. Belge Micro. 19: 98.

Constantineau, 1901, Rev. Gen. Bot. 13: 379.

Atkinson, 1909, Ann. Mycol. 7: 450.

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Sparrow, 1932, Mycologia 24: 289.

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Domjan, 1935, Folio Cryptogam. 2: 31.

Cook, 1932, New Phytol. 31: 142. 1933, Glamorgan County Nat. Hist. 1: 214. 1935, Arch. Protistk. 86: 63.

*Lagenidium entophytum*

Zopf, 1884, Nova Acta Ksl. Leop.-Carol. Deut. Akad. Nat. 47: 154.

De Wildeman, 1891, Bull. Soc. Roy. Bot. Belg. 30: 138. 1893, Ann. Soc. Belge Micro. 17: 10, 46. 1895, Mem. Soc. Belge Micro. 19: 100.

*Lagenidium americanum*

Atkinson, 1909, Bot. Gaz. 48: 331.

*Pythium entophytum*

Pringsheim, 1858, Jahrb. Wiss. Bot. 1: 287, 305.

*Lagenidium gracile*

Zopf, 1884, Nova Acta Ksl. Leop.-Carol. Deut. Akad. Nat. 47: 158.

De Wildeman, 1895, Mem. Soc. Belge Micro. 19: 102.

Cook, 1932, New Phytol. 31: 140. 1935, Arch. Protistk. 86: 88.

- Lagenidium papillosum*  
Cocconi, 1894. Mem. R. Accad. Sci. Inst. Bologna  
4: 362.
- Myzocytium proliferum*  
Schenk, 1858. Über das Vorkommen Contractiler Zellen im Pflanzenreich, p. 10. 1858, Verh. Phys.-Med. Gesell. 8: XXVII. 1859, *Ibid.* 9: 27.  
Cornu, 1869. Bull. Soc. Bot. France 16: 222.  
Zopf, 1884. Nova Acta Ksl. Leop.-Carol. Deut. Akad. Nat. 47: 159.  
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Skvortzow, 1927. *Ibid.* 57: 206.  
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- Pythium globosum*  
Schenk, 1858. Verh. Phys.-Med. Gesell. 9: 27.
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- Lagenidium globosum*  
Lindstedt, 1872. Synopsis d. Saproleg., p. 54.
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Chaudhuri, 1931. Arch. Protistk. 75: 472.  
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*Lagenidium americanum*  
Atkinson, 1909. Bot. Gaz. 48: 334.
- Spirogyra grevilleana*  
*Lagenidium gracile*  
De Wildeman, 1895. Mem. Soc. Belge Micro. 19: 102.
- Spirogyra insignis*  
*Lagenidium americanum*  
Atkinson, 1909. Bot. Gaz. 48: 334.
- Spirogyra jurgensii*  
*Myzocytium proliferum*  
Tokunaga, 1934. Trans. Sapporo Nat. Hist. Soc. 13: 229.
- Spirogyra mirabilis*  
*Lagenidium rabenhorstii*  
Domjan, 1935. Folio Crypt. 2: 31.
- Spirogyra orthospira*  
*Lagenidium rabenhorstii*  
Graff, 1928. Mycologia 20: 169.
- Spirogyra varians*  
*Lagenidium americanum*  
Atkinson, 1909. Bot. Gaz. 48: 334.  
*L. rabenhorstii*  
De Wildeman, 1891. Bull. Soc. Belge Micro. 16: 138.
- Zygnema sp.*  
*Lagenidium rabenhorstii*  
Domjan, 1935. Folio Crypt. 2: 31.
- Myzocytium proliferum*  
Schenk, 1858. Über das Vorkommen Contracteler Zellen im Pflanzenreich, p. 10.  
Zopf, 1884. Nova Acta Ksl. Leop.-Carol. Deut. Akad. Nat. 47: 159.  
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Cejp, 1935. Bull. Int. l'Acad. Sci. Bohême 1935: 7.
- Pythium proliferum*  
Walz, 1870. Bot. Zeit. 28: 556.
- Pythium globosum*  
Walz, i.e., p. 556.
- Zygnema cruciatum*  
*Myzocytium proliferum*  
Graff, 1928. Mycologia 20: 168.
- Desmidaceae*
- Arthrodeshmus* sp.  
*Bicerium nuso*  
Sorokin, 1883. Arch. Bot. Nord France 2: 44. 1889, Rev. Mycol. 11: 138.
- Closterium* sp.  
*Lagenidium Closterii*  
Petersen, 1910. Ann. Mycol. 8: 537.  
Cejp, 1933. Bull. Int. l'Acad. Bohême, 1933: 7. 1933, *Ibid.* p. 9.  
Couch, 1935. Mycologia 27: 384.
- Lagenidium intermedium*  
Cejp, 1935, i.e., p. 8.  
De Wildeman, 1893. Ann. Soc. Belge Micro. 17: 54. 1895, *Ibid.* 19: 78.
- Myzocytium megastomum* de Wildeman forma Skvortzow, 1925. Arch. Protistk. 51: 431.
- Myzocytium (Aencylistees) miurii*  
Skvortzow, 1925, i.e., p. 432.
- Myzocytium proliferum*  
Cejp, 1932. Bull. Int. l'Acad. Bohême 1932: 5.
- Closterium acerosum*  
*Myzocytium proliferum*  
Sparrow, 1932. Mycologia 24: 288.
- Closterium areolatum*  
*Myzocytium megastomum*  
Berdan, 1938. Mycologia 30: 408.
- Closterium attenuatum*  
*Myzocytium megastomum*  
De Wildeman, 1893. Ann. Soc. Belge Micro. 17: 55.
- Closterium didymotocum*  
*Myzocytium proliferum*  
Reinsch, 1878. Jahrb. Wiss. Bot. 11: 300.
- Closterium ehrenbergii*  
*Lagenidium intermedium*  
De Wildeman, 1895. Ann. Soc. Belge Micro. 19: 96.
- Closterium leiblinii*  
*Myzocytium proliferum*  
Cejp, 1932. Bull. Int. l'Acad. Bohême 1932: 5.
- Closterium ralfsii* var. *hybridum*  
*Lagenidium saccaloides*  
Serbinow, 1924. La Defense des Plantes 1: 85.
- Closterium striolatum*  
*Lagenidium Closterii*  
De Wildeman, 1893. Ann. Soc. Belge Micro. 17: 42.
- Myzocytium megastomum*  
Berdan, 1938. Mycologia 30: 408.
- Cosmarium* sp.  
*Myzocytium irregularare*  
Cejp, 1935. Bull. Int. l'Acad. Bohême 1935: 7.
- Cosmarium Botrytis*  
*Myzocytium proliferum*  
Reinsch, 1878. Jahrb. Wiss. Bot. 11: 300.

- Cosmarium connatum*  
*Myzocytium proliferum*  
 Reinsch, 1878, I.c., p. 300.
- Cosmarium pyramidatum*  
*Lagenidium pygmaeum*  
 Schultz-Danzig, 1923, Schr. f. Süssw.-und Meeresk. 11: 179.
- Cosmarium planula*  
*Myzocytium proliferum (?)*  
 Reinsch, 1878, Jahrb. Wiss. Bot. 11: 300.
- Dociodium ehrenbergii*  
*Mitochytridium ramosum*  
 Dangeard, 1911, Bull. Soc. Mycol. France 27: 202.  
 Couch, 1935, Jour. Elisha Mitchell Sci. Soc. 51: 293.
- Euastrum sp.*  
*Myzocytium proliferum*  
 De Wildeman, 1893, Ann. Soc. Belge Micro. 19: 77.
- Euastrum humerosum*  
*Lagenidium entophytum*  
 Schultz-Danzig, 1923, Schr. f. Süssw.-und Meeresk. 11: 180.
- Euastrum oblongum*  
*Lagenidium sp.*  
 De Wildeman, 1893, Ann. Soc. Belge Micro. 19: 75.
- Microasterias sp.*  
*Myzocytium irregularare*  
 Petersen, 1909, Bot. Tidsskr. 29: 403. 1910, Ann. Mycol. 8: 539.
- Microasterias mahabuleshwarensis* var. *wallichii*  
*Lagenidium entophytum*  
 Schultz-Danzig, 1923, Schr. f. Süssw.-und Meeresk. 11: 180.
- Microasterias rotata*  
*Myzocytium proliferum*  
 Reinsch, 1878, Jahrb. Wiss. Bot. 11: 300.
- Myzocytium irregularare*  
 Cejp, 1933, Bull. Int. l'Aead. Sci. Bohême 1933: 8. 1935, Ibid. p. 7.
- Microasterias truncata*  
*Myzocytium irregularare*  
 Cejp, 1935, Ibid. p. 7.
- Pennium digitus*  
*Lagenidium sp.*  
 Scherffel, 1926, Arch. Protistk. 51: 246.
- Pleurotaenium sp.*  
*Myzocytium irregularare*  
 Cejp, 1935, I.c., p. 7.
- Pleurotaenium ehrenbergii*  
*Iaphanomyopsis bacillariacearum (?)*  
 West and West, 1906, Trans. Roy. Irish Acad. B, 33: 77.
- Pleurotaenium trabecula*  
*Lagenidium intermedium*  
 Cejp, 1935, I.c., p. 8.
- Spirotaenia sp.*  
*Myzocytium megastomum*  
 De Wildeman, 1893, Ann. Soc. Belge Micro. 17: 56.
- Spirotaenia condensata*  
*Myzocytium sp.*  
 Scherffel, 1926, Arch. Protistk. 51: 246.
- Staurastrum sp.*  
*Myzocytium proliferum*  
 Scherffel, 1926, I.c., p. 246.
- Chaetophoraceae*
- Draparnaldia glomerata*  
*Pseudolpidium deformans*  
 Serbinow, 1907, Scripta Bot. Hort. Imp. Univ. Petrop. 24: 25.
- Oedogoniaceae*
- Oedogonium sp.*  
*Myzocytium sp. (?)*  
 Turner, 1892, Kgl. Svensk. Vetens. Akad. Hand. n.f. 25 no. 5: 164.
- Lagenidium rabenhorstii*  
 Petersen, 1909, Bot. Tidsskr. 9: 400. 1910, Ann. Mycol. 8: 536.
- L. zoppii*  
 De Wildeman, 1891, Bull. Soc. Belge Micro. 16: 139.  
 Petersen, 1909, Bot. Tidsskr. 29: 401.
- L. syncytiorum*  
 Klebahn, 1892, Jahrb. Wiss. Bot. 24: 263.
- L. marchaliuum*  
 De Wildeman, 1897, Ann. Soc. Belge Micro. 21: 8.  
 Couch, 1935, Mycologia 27: 384.
- L. Oedogonii*  
 Scherffel, 1902, Hedwigia 41: (105). 1925, Arch. Protistk. 52: 109.  
 Couch, 1935, Mycologia 27: 386.
- Lagenidium sp.*  
 Couch, 1935, I.c., p. 385.
- Olpidiopsis Oedogoniorum*  
 Scherffel, 1925, Arch. Protistk. 52: 109.  
 Sparrow, 1933, Mycologia 25: 516.
- O. fusiformis* var. *Oedogoniarum*  
 Sorokin, 1883, Arch. Bot. Nord France 2: 29. 1889, Rev. Mycol. 11: 89.
- Olpidium Oedogoniarum (?)*  
 De Wildeman, 1894, Ann. Soc. Belge Micro. 18: 154.
- Reticularia Oedogonii*  
 Skvortzow, 1925, Arch. Protistk. 51: 432.
- Oedogonium bosci*  
*Lagenidium syncytiorum*  
 Klebahn, 1892, Jahrb. Wiss. Bot. 24: 263.
- Oedogonium crassusellum* var. *idiosporium*  
*Woronina polycystis*  
 Cook, 1932, New Phytol. 31: 134.
- Oedogonium franklinianum*  
*Lagenidium sp. (?)*  
 Scherffel, 1926, Arch. Protistk. 51: 246.
- Oedogonium obsidionale*  
*Achlyogeton solatum*  
 Cornu, 1870, Bull. Soc. Bot. France 17: 298.
- Oedogonium orthospira*  
*Lagenidium rabenhorstii*  
 Graff, 1928, Mycologia 20: 169.
- Cladophoraceae*
- Chaetomorpha aerea*  
*Lagenidium sp.*  
 Deckenbach, 1903, Flora 92: 278.

- Cladophora sp.  
*Achlyogoton entophysum*  
 Schenk, 1859. Bot. Zeit. 17: 399.  
 Sorokin, 1876. Ann. Sci. Nat. 6 ser. 4: 63. 1883, Arch. Bot. Nord France 2: 44. 1889, Rev. Mycol. 11: 139.  
 Martin, 1927. Mycologia 19: 188.  
 Tokunaga, 1934. Trans. Sapporo Nat. Hist. Soc. 13: 227.
- Biericium transversum*  
 Sorokin, 1883. Arch. Bot. Nord France 2: 43. 1889, Rev. Mycol. 11: 138.
- Myzocytium proliferum*  
 Walz, 1870. Bot. Zeit. 28: 553.  
 Martin, 1927. Mycologia 19: 188.  
 Tokunaga, 1934. Trans. Sapporo Nat. Hist. Soc. 13: 228.
- Siroplidium Bryopsidis*  
 Sparrow, 1936. Biol. Bull. 70: 252.
- Cladophora flavaescens  
*Achlyogoton salinum*  
 Dangeard, 1932. Le Bot. 24: 240.
- Cladophora kuetzingiana  
*Myzocytium proliferum*  
 Graff, 1928. Mycologia 20: 168.
- Cladophora laetevirens  
*Achlyogoton salinum*  
 Dangeard, 1932. Le Bot. 24: 240.
- Bryopsidaceae*
- Bryopsis plumosa  
*Olpidium Bryopsidis*  
 De Bruyne, 1890. Arch. Biol. 10: 85.  
*Siroplidium Bryopsidis* (de Bruyne)  
 Petersen, 1905. Overs. Kgl. Dansk. Vids. Selsk. Forh. no. 5: 479.  
 Sparrow, 1934. Dansk. Bot. Ark. 8, no. 6: 9. 1936, Biol. Bull. 70: 252.
- Vaucheria sp.  
*Woronina glomerata*  
 Scherffel, 1925. Arch. Protistk. 52: 59.  
 Valkanov, 1931. Ibid. 73: 361. 1940, Ibid. 93: 240.
- Vaucheria sessilis  
*Chytridium glomeratum*  
 Cornu, 1872. Ann. Sci. Nat. 5 ser. 15: 187.  
*Woronina glomerata* (Cornu)  
 Fischer, 1892. Rabenhorst's Kryptfl. 1, 4: 64.  
 Zopf, 1894. Phys. Morph. Med. Organismen 2: 46.  
 Tokunaga, 1933. Trans. Sapporo Nat. Hist. Soc. 13: 26.
- Vaucheria terrestris  
*Chytridium glomeratum*  
 Cornu, 1872. Ann. Sci. Nat. 5 ser. 15: 187.  
*Woronina glomerata* (Cornu)  
 Fischer, 1892. Rabenhorst's Kryptfl. 1, 4: 64.  
 Zopf, 1894. Phys. Morph. Nied. Organismen 2: 46.
- Characeae*
- Chara sp.  
*Lagenidliopsis reducta*  
 De Wildeman, 1896. Ann. Soc. Belge Micro. 20: 109.
- PHAEOPHYCEAE**
- Ectocarpaceae*
- Akinetospora sp.  
*Eurychasma dicksonii*  
 Petersen, 1905. Overs. Kgl. Dansk. Vids. Selsk. Forh. 5: 477.
- Ectocarpus sp.  
*Eurychasma dicksonii*  
 Petersen, 1905, l.c., p. 476.  
 Johnson, 1909. Sci. Proc. Roy. Dublin Soc. 12: 142.  
 Dangeard, 1934. Ann. Protist. 4: 69.  
*Petersenia andreei*  
 Sparrow, 1934. Dansk. Bot. Ark. 8, no. 6: 17.
- Ectocarpus confervoides  
*Rhizophidium dicksonii*  
 Hauck, 1878. Oesterr. Bot. Zeitschr. 28: 321.
- Eurychasma dicksonii*  
 Petersen, 1905. Overs. Kgl. Dansk. Vids. Selsk. Forh. 5: 477.
- Ectocarpus crinitus  
*Rhizophidium dicksonii*  
 Hauck, 1878. Oesterr. Bot. Zeitschr. 28: 321.  
 Wright, 1879. Trans. Roy. Irish Acad. 26: 369.
- Ectocarpus sandrianus  
*Eurychasma dicksonii*  
 Petersen, 1905. Overs. Kgl. Dansk. Vids. Selsk. Forh. 5: 477.
- Ectocarpus granulosus  
*Rhizophidium dicksonii*  
 Wright, 1879. Trans. Roy. Irish Acad. 26: 369.
- Ectocarpus sandrianus  
*Eurychasma dicksonii*  
 Petersen, 1905. Overs. Kgl. Dansk. Vids. Selsk. Forh. 5: 477.
- Ectocarpus siliculosus  
*Rhizophidium dicksonii*  
 Rattray, 1884. Trans. Edinburgh Roy. Soc. 32: 589.  
*Petersenia andreei*  
 Sparrow, 1936. Biol. Bull. 70: 245.
- Pylaiella littoralis  
*Rhizophidium dicksonii*  
 Wright, 1879. Trans. Roy. Irish Acad. 26: 369.  
 Wille, 1899. Vids. Selsk. Math.-Nat. Klasse I, 3: 2.  
 Lowenthal, 1905. Arch. Protistk. 5: 225.  
*Eurychasma dicksonii*  
 Petersen, 1905. Overs. Kgl. Dansk. Vids. Selsk. Forh. 5: 476.
- Striaria attenuata  
*Rhizophidium dicksonii*  
 Wright, 1879. Trans. Roy. Irish Acad. 26: 369.  
 Hauck, 1878. Oesterr. Bot. Zeitschr. 28: 321.
- Striaria attenuata var. fragilis  
*Olpidium dicksonii* var. *Striariae*  
 Wille, 1899. Vid. Selsk. Math.-Nat. Klasse I, 3: 2.
- Stictyosiphon corbierei  
*Eurychasma dicksonii*  
 Dangeard, 1934. Ann. Protist. 4: 69.
- Stictyosiphon tortilis  
*Eurychasma dicksonii*  
 Petersen, 1905. Overs. Kgl. Dansk. Vids. Selsk. Forh. 5: 477.
- RHODOPHYCEAE**
- Ceramiales*
- Callithamnion corymbosum  
*Pleotrichelus lobatus*  
 Petersen, 1905. Overs. Kgl. Dansk. Vids. Selsk. Forh. 5: 460.

*Callithamnion hookeri*

*Pleotrichelus lobatus*

Petersen, 1905, l.c., p. 462.

*Callithamnion roseum*

*Petersenia lobata*

Sparrow, 1936, Biol. Bull. 70: 245.

*Ceramium sp.*

*Pontisma lagenidioides*

Petersen, 1905, Overs. Kgl. Dansk. Vids. Selsk. Forh. 5: 182.

*Pleotrichelus (Petersenia) pollagaster*

Sparrow, 1934, Dansk. Bot. Ark. 8, no. 6: 15.

*Ceramium acanthonotum*

*Chytridium tumifaciens*

Magnus, 1872a, Sitzb. Gesell. Nat. Freunde Berlin 1872: 87, 1872b, Jahresb. Komm. Untersuch. Deut. Meere Kiel 2: 76, 1873, Hedwigia 12: 28.

*Ceramium diaphanum*

*Pontisma lagenidioides*

Sparrow, 1936, Biol. Bull. 70: 252.

*Eurychasmidium tumifaciens*

Sparrow, 1936, l.c., p. 241.

*Petersenia sp.*

Sparrow, 1936, l.c., p. 243.

*Ceramium flabelligerum*

*Chytridium tumifaciens*

Magnus, 1872a, Sitzb. Gesell. Nat. Freunde Berlin 1872: 87, 1872b, Jahresb. Komm. Untersuch. Deut. Meere Kiel 2: 76, 1873, Hedwigia 12: 28.

*Olpidium tumifaciens*

Fischer, 1892, Rabenhorst's Krypt'fl. I, 4: 27.

*Eurychasmidium tumifaciens*

Sparrow, 1936, Biol. Bull. 70: 241.

*Ceramium fructiculosum*

*Pontisma lagenidioides*

Sparrow, 1934, Dansk. Bot. Ark. 8, no. 6: 11.

*Ceramium rubrum*

*Pontisma lagenidioides*

Petersen, 1905, Overs. Kgl. Dansk. Vids. Selsk. Forh. 5: 182.

*Pleotrichelus pollagaster*

Petersen, 1905, l.c., p. 462.

*Ceramium tenuissimum*

*Pontisma lagenidioides*

Petersen, 1905, l.c., p. 482.

*Scirospora interrupta*

*Petersenia lobata*

Feldmann, 1940, Bull. Soc. Hist. Nat. Afrique Nord 31: 72.

*Spermothamnion repens*

*Petersenia lobata*

Sparrow, 1934, Dansk. Bot. Ark. 8, no. 6: 13.

*Spermothamnion turneri*

*Pleotrichelus lobatus*

Petersen, 1905, Overs. Kgl. Dansk. Vids. Selsk. Forh. 5: 460.

*Rhodymeniaceae*

*Halosaccion ramentaceum*

*Eurychasma sacculus*

Petersen, 1905, l.c., p. 477.

*Rhodomenia palmata*

*Eurychasma sacculus*

Petersen, 1905, l.c., p. 477.

*Rhodophyllidiaceae*

*Cystoclonium purpurascens*

*Pyrrhosorus marinus*

Juel, 1901, Bih. Kgl. Svensk. Vet.-Akad. Hand. 26, afd. III, no. 14: 14, 1901, Rev. Mycol. 21: 111.

## BRYOPHYTA

### HEPATICEAE

*Ricciaceae*

*Riccia sp.*

*Olpidiopsis Riccieae*

Du Plessis, 1933, Ann. Bot. 47: 761.

*Musci*

Unidentified moss species

*Lagenidium ellipticum*

De Wildenau, 1893, Ann. Soc. Belge Micro. 17: 5, 1893, Jour. Roy. Micro. Soc. 1893: 765.

## SPERMATOPHYTA

### GYMNOSPERMACEAE

*Pinaceae*

*Abies canadensis*

*Lagenidium pygmaeum*

Karling, 1941, Mycologia 33: 358.

*Pinus sp.*

*Lagenidium pygmaeum*

Schultz-Danzig, 1923, Schr. Süßw.-und Meerest. 11: 180.

*Pinus austriaca*

*Lagenidium pygmaeum*

Zopf, 1887, Abh. Nat. Gesell. Halle 17: 97, Karling, 1941, l.c., p. 358.

*Pinus austriaca var. nigra*

*Lagenidium pygmaeum*

Karling, 1941, l.c., p. 358.

*Pinus banksiana*

*Lagenidium pygmaeum*

Karling, 1941, l.c., p. 358.

*Pinus densiflora*

*Lagenidium pygmaeum*

Karling, 1941, l.c., p. 358.

*Pinus laricio*

*Lagenidium pygmaeum*

Zopf, 1887, l.c., p. 97.

*Pinus pallasiana*

*Lagenidium pygmaeum*

Zopf, 1887, l.c., p. 97.

*Pinus strobus*

*Lagenidium pygmaeum*

Karling, 1941, l.c., p. 358.

*Pinus sylvestris**Lagenidium pygmaeum*

Zopf, 1887. Abh. Nat. Gesell. Halle 17: 97.

Karling, 1941, l.c., p. 358. 1941, Torreya 41: 108.

*Pinus thunbergii**Lagenidium pygmaeum*

Karling, 1941. Mycologia 33: 358.

## Unidentified conifer pollen grains

*Lagenidium pygmaeum*

Maurizio, 1895. Jahrsb. Nat. Gesell. Graubündens 39:14.

De Wildeman, 1895. Ann. Soc. Belge Micro. 19: 68.

Petersen, 1909. Bot. Tidsskr. 29: 401. 1910, Ann. Mycol. 8: 537.

## ANGIOSPERMAE

## Gramineae

*Agropyron repens**Lagena radicicola*

Vanterpool and Ledingham, 1930. Canad. Jour. Res. 2: 177.

Truscott, 1933. Mycologia 25: 263.

*Hordeum vulgare**Lagena radicicola*

Vanterpool and Ledingham, 1930, l.c.

*Saccharum officinarum**Chytrid* sp.

Carpenter, 1940. The Hawaiian Planter's Record 1: 44.

*Secale cereale**Lagena radicicola*

Vanterpool and Ledingham, 1930, l.c.

*Triticum aestivum**Lagena radicicola*

Vanterpool and Ledingham, 1930, l.c.

*Triticum durum**Lagena radicicola*

Vanterpool and Ledingham, 1930, l.c.

*Zea mays**Lagena radicicola*

Vanterpool and Ledingham, 1930, l.c.

## Other wild grasses

*Lagena radicicola*

Truscott, 1933, l.c., p. 263.

## Ulmaceae

*Ulmus americana**Carpenterella molinea*

Tehon, L. R., and H. A. Harris, 1941. Mycologia 33: 128.

## Solanaceae

## Nicotiana sp. (?)

*Myzocytium* sp. (?)

Preissecker, 1905. Fachl. Mitteil. Oesterr. Tabakregie 5, heft. 1: 3.

## Caryophyllaceae

*Stellaria media**Myzocytium* sp. (?)

Barrett, 1935. Phytopath. 25: 898.

## ANIMALS

## INFUSORIA

## Vorticella sp.

*Ectrogella perforans*

Sparrow, 1936. Biol. Bull. 70: 241.

## Vorticella microsoma

*Myzocytium* sp. (?)

Stein, 1851. Zeitschr. Wiss. Zool. 3: 476. 1854, Die Infusionsthiere und ihre Entw. Leipzig.

## Vorticella nebulifera

*Myzocytium* sp. (?)

Stein, 1859. Der Organismus der Infusionsthiere. 1 abt., p. 106.

## ROTATORIA

## Philodina rosetta

*Chytridium elegans*

Perroncito, 1888. Centralbl. Bakt. Parasitk. 4: 295.

*Woronina elegans*

Fischer, 1892. Rabenhorst's Krypt'fl. I, 4: 66.

## Unidentified rotifers, eggs, and embryos

*Petersenia* sp. (?)

Sparrow, 1936. Biol. Bull. 70: 244.

*Myzocytium zoophthorum*

Sparrow, 1936. Jour. Linn. Soc. London Bot. 50: 461.

*Lagenidium oophilum*

Sparrow, 1939. Mycologia 31: 531.

*Lagena oophilum*

Sparrow, 1939, l.c.

## NEMATODA

## Anguillula sp.

*Achlyogeton* (?) *rostratum*

Sorokin, 1876. Ann. Sci. Nat. 6 ser. 1: 64.

*Myzocytium proliferum* var. *vermiculum*

Zopf, 1884. Nova Acta Ksl. Leop.-Carol. Deut. Akad. Nat. 47: 167.

*Myzocytium vermiculum*

Fischer, 1892. Rabenhorst's Krypt'fl. I, 4: 75.

Dangeard, 1906. Le Bot. 9: 207.

*Bericium lethale*

Sorokin, 1883. Arch. Bot. Nord France 2: 37. 1889, Rev. Mycol. 11: 138.

*Protasceus subuliformis*

Dangeard, 1903. C. R. Acad. Sci. Paris 136: 628. 1906, Le Bot. 9: 256.

## Rhabditis dolichura

*Protasceus subuliformis*

Maupas, 1915. Bull. Soc. Hist. Nat. Afric. 6: 34.

*Protasceus subuliformis* var. *maupasii*

Maire, 1915. Ibid. 6: 50.

## Rhabditis giardi

*Protasceus subuliformis*

Maupas, 1915, l.c., p. 34.

*Protasceus subuliformis* var. *maupasii*

Maire, 1915, l.c., p. 50.

## Rhabditis teres

*Protasceus subuliformis*

Maupas, 1915, l.c., p. 34.

*Protasceus subuliformis* var. *maupasii*

Maire, 1915, l.c., p. 50.

## Unidentified nematodes

*Myzocytium vermicolum*

Valkanov, 1931, Arch. Protistk. 73: 365.

## DIPTERA

## Mosquito larvae

*Lagenidium giganteum*

Couch, 1935, Mycologia 27: 376.

Matthews, 1935, Jour. Elisha Mitchell Sci. Soc. 51: 309.

## Dipterous pupae

*Myrophagus ucrainicus*

Sparrow, 1939, Mycologia 31: 443.

Petch, 1940, The Naturalist no. 998: 68.

*Entomophthora (Tarichium) reticulata*

Petch, 1939, Trans. Brit. Mycol. Soc. 23: 127.

## COLEOPTERA

## Acanthonomus grandis

*Pseudalpidium* sp. (?)

Krafska and Miller, 1926, Ann. Entomol. Soc. of America 19: 464.

*Anisplia austriaca**Olpidiopsis (?) ucrainica*

Wize, 1901, Bull. Inter. L'Acad. Sci. Cracovie 1901: 713.

## Cleonus punctiventris

*Olpidiopsis (?) ucrainica*

Wize, 1901, i.e., p. 713.

## CRUSTACEAE

## Cyclops sp.

*Blastulidiopsis chattoni*

Sigot, 1931, C. R. Soc. Biol. 108: 37.

## Daphne sp.

*Lagenidium giganteum*

Couch, 1935, Mycologia 27: 376.

## Unidentified copepods

*Lagenidium giganteum*

Couch, 1935, i.e., p. 376.

## Callinectes sapidus

*Lagenidium Callinectes*

Couch, 1942, Jour. Elisha Mitchell Sci. Soc. 58: 158.

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